ECOLOGICAL MONOGRAPHS

VOL. I APRIL, 1931 NO. 2

OFFICIAL PUBLICATION OF THE
ECOLOGICAL SOCIETY OF AMERICA

CONTENTS

PUBLISHED QUARTERLY BY
THE DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

Issued on the fifteenth of December, March, June, and September

The editorial board of this journal will consider ecological papers which are long enough to make twenty-five printed pages or more. Shorter ecological papers should be submitted to the editor of *Ecology,* which is also published by the Ecological Society of America. Both journals are open to ecological papers from all fields of biological science.

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Application for entry as second-class matter is pending.

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THE VEGETATION OF OKLAHOMA

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THE VEGETATION OF OKLAHOMA

Introduction

In traveling across the state of Oklahoma from east to west, one first enters a well developed deciduous forest which clothes the rugged, mountainous topography. Should the journey begin in the southeast, a magnificent forest of short-leaf pine would be encountered. Here one treads on a carpet of fallen needles beneath the towering pines and the way is unobstructed in the somber forest depths by shrubs or other undergrowth. The pine forest, however, is of limited extent and forests of pines intermixed with various oaks and hickories are of much more frequent occurrence. In fact, the hardwood forests, often with only a sprinkling of evergreens, predominate in the extreme eastern portion of the state. A damp, spongy layer of decaying leaf-mold covers the soil and where enough light filters through the leafy canopy a shrubby and herbaceous vegetation abounds. Where the forest is denser, there is found only a scattered growth of perennial herbs, which develop in spring before the leafy canopy of the trees, and a few shade enduring ferns, mosses, and fungi.

Along the streams a great variety of woody plants occurs. In low places in the extreme southeast, miniature cypress swamps are found. The tall trees with buttressed bases produce an atmosphere which is strongly suggestive of the typical cypress swamps farther southward. Groves of tall, straight red gums may be seen; some fine specimens with diameters of four to five feet and a hundred feet high still occur. They have escaped the ax of the lumberman because of the inaccessibility of the region which is a result of the rough topography. But all of the best and most accessible timber has been cut and to find undisturbed primeval forest one must travel far from the highways.

Proceeding westward, the forest becomes less luxuriant with decrease in rainfall. Woodland intergrades into scrub and on soils less favorable to woody plants openings of grassland occur. The forest gradually becomes poorer in species and dwarfed in stature, and scrub and grassland become more and more abundant. This condition prevails until nearly half the length of the state has been traversed and then, rather abruptly, largely on account of change in water content with different types of soil, a transition from alternating forest-scrub and prairie to almost continuous grassland occurs.

The grassland consists of tall, sod-forming species which more or less completely cover the ground. Chief among these are the bluestems, dropseeds, etc., interspersed with an abundance of legumes, composites, and

numerous other prairie forms. Where overgrazing has occurred, the tall grasses have largely been replaced by the short grasses; blue grama and buffalo grass being especially important. These form dense mats only three to four inches high and give a monotonous appearance to the landscape.

A more careful scrutiny reveals almost endless details concerning the arrangement or grouping of plants, which may be attributed to local conditions and to community relationships. The local dominance of non-grassy species in the prairie constantly changes. Spring societies of anemones, spiderworts, wild onions, etc., may characterize the landscape for many miles. They are later replaced by summer-blooming species, of which the psoraleas and prairie clovers are representative. Even in the fall when the dominant grasses reach their maximum development, herbaceous societies such as goldenrods, asters, and other late blooming forms are abundant.

With increasing aridity westward, the tall grasses and their associates are less thrifty. All but the more drought-resistant finally disappear. Thus a gradual change from tall-grass prairie to one in which tall grasses are regularly intermixed with short grasses occurs. The first appearance of short grasses is found on thinner soils of exposed areas, but they gradually increase in abundance and replace the tall grasses until finally the latter are found only in areas having the highest water content. Outstanding exceptions to the general rule are areas of tall grasses many miles in extent which cover the sandy tracts that lie in a more or less northwest to southeast direction, especially north of the sand-choked rivers from whose dry beds the sand has been blown. The mesic associates of the tall grasses are unable to withstand the increasing drought. At first they become dwarfed but later entirely disappear. They are replaced in part by drought-resistant, western species but in general the more xeric, western prairies have a smaller number of societies than the moister ones eastward. Thus the tall-grass or true prairie gradually changes to a mixed type of grassland where short grasses intermingle with a scattered growth of the taller ones. The mixed prairie, in turn, under increasing aridity, gives way to the short-grass plains.

Ribbon-like belts of forest extend along the streams far into the grassland. Their dark green verdure contrasts sharply with the lighter green of the grasses and adds variety to the level or rolling prairie landscape. These tongues of woodland have their origin in the deep, dense forests of the eastern part of the state. Westward, the trees decrease in size, number of species, and luxuriance of growth. With decrease in height, the tops become low and bushy and are relatively more widely spread. Many species of the mesic eastern forest reach their western limit and their place is taken by others of greater drought resistance which make up the major portion of the forests along the streams in the central part of the state. Kentucky coffee tree, pecan, and yellow oak, for example, soon reach their western limit but black walnut and bur oak extend well into west-central Oklahoma. The elm and ash have

migrated somewhat farther westward and after their disappearance the cottonwood and willows alone form a narrow and intermittent fringe of trees along the stream banks in the arid west. In the extreme western portion of the state there is little to relieve the monotony of the landscape. Trees occur only sparsely even on the flood plain and vast stretches of short grasses are here and there interrupted by cacti, yuccas, and the widely scattered mesquite.

This study was suggested by Dr. J. E. Weaver. To him the writer wishes to acknowledge his gratitude for outlining the methods of investigation and for efficient direction throughout the field work, as well as for much help in the organization and presentation of the results. The writer is also indebted to Prof. T. J. Fitzpatrick for careful reading of the manuscript.

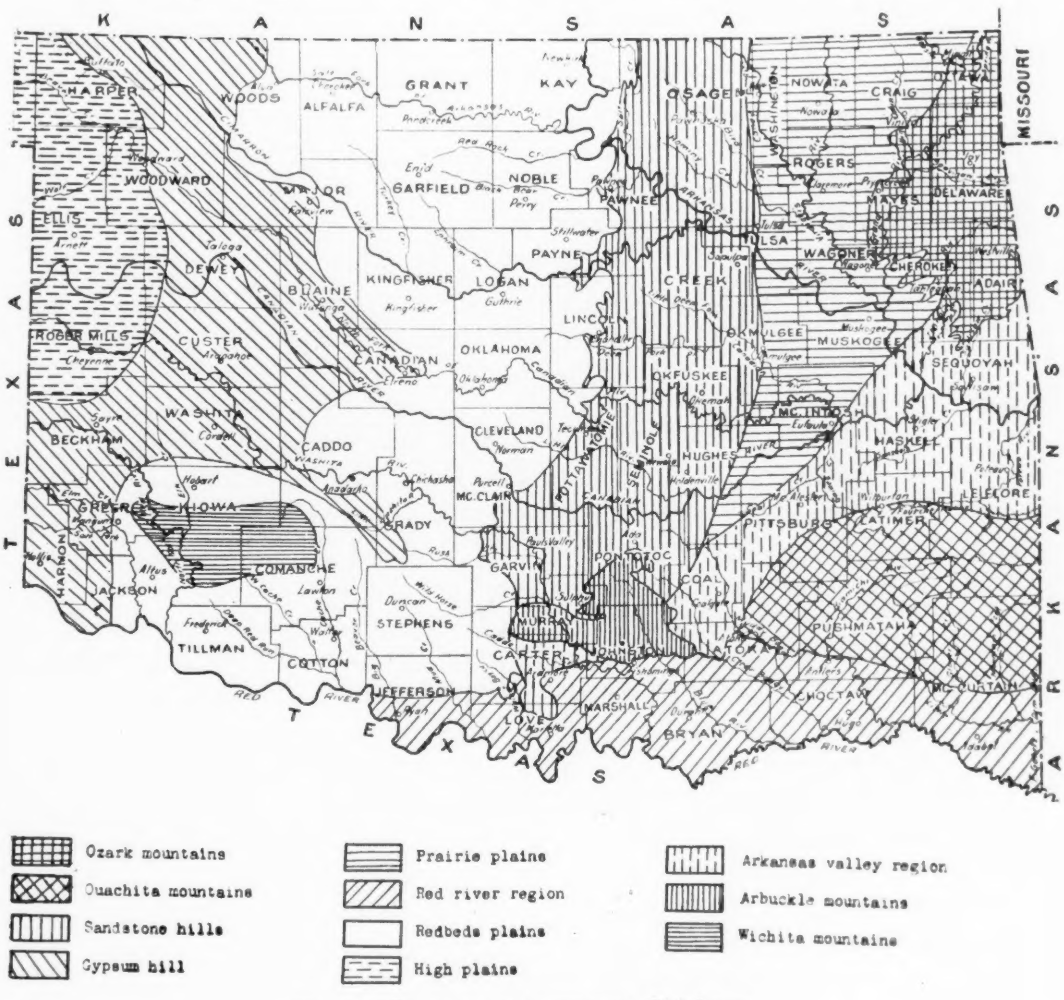

FIG. 1. Physiographic map of Oklahoma.

LOCATION AND EXTENT OF AREA

The region studied covers an area of 70,740 square miles. It is bounded on the south by the Red River (Fig. 1). This stream flows southeastward

about one-third of the way along the southern boundary of the state, then, after crossing the 34th parallel at the 98th meridian, its course is nearly due eastward. The northern boundary is the 37th parallel of latitude; hence the state is about 225 miles wide. The eastern side, bounded by Missouri and Arkansas, is not a straight line but approximates 94° 30′ longitude. The 100th meridian forms the western boundary except in the north where the "panhandle" extends to the 103rd degree. This portion of the state is only 34 miles wide but it increases the length of the state from 320 to 470 miles. Within the area thus delimited the general slope, as indicated by the main river courses, is from northwest to southeast. The high plains along the western border with an elevation of 4,500 feet exceed in altitude the Ozark and Ouachita Mountains in the east.

Physiographic Regions and Topography

Topographically the state of Oklahoma is a plain which, with many interruptions, slopes from northwest to southeast. It includes eleven distinct physiographic provinces (Fig. 1). The Ozark Mountains in the northeast extend about 85 miles from north to south and have a width of about 35 miles in the central portion. The elevation ranges from 600 feet in the valleys to a maximum of 1,100 feet. The rough topography has resulted from the erosion of a former plain. It is underlaid by Mississippian cherts and limestones of the Boone formation. The streams have cut narrow, steep-sided valleys to a maximum depth of 400 feet, thus producing a mountainous topography. Remnants of the plain persist in the form of flat-topped hills which have moderately deep, fertile soil. The steep slopes are covered with a rocky layer of loose fragments of chert. A well developed oak-hickory forest covers most of the area, but on many of the rocky slopes it is intermixed with pine, and small areas of grassland occur in openings.

The Ouachitas form the largest mountainous area. They occupy a region nearly 50 miles wide which extends westward from Arkansas into the southeast corner of the state to a distance of 90 miles. They constitute the most rugged region of Oklahoma. Standley shale and Jackfork limestone, also Mississippian strata, are the most important underlying rocks. The unequal weathering of the broken and folded bedrock has resulted in the present mountainous topography. The resistant peaks of Jackfork limestone reach a maximum elevation of 3,000 feet above sea level. The greatest extreme of elevation is that of Rich Mountain which towers 2,000 feet above the valley floor. Oak forests dominate but admixtures of pine are common on rocky slopes and in the extreme southeast the pines completely occupy certain areas.

The Lower Arkansas Valley Region lies in the central part of eastern Oklahoma and separates the Ozark and Ouachita Mountains. It is 50 miles wide near the eastern boundary but in the western part decreases to a width

of 20 miles. Weathering of the Pennsylvanian sandstones and shales has given rise to a rather rough topography. Broad, deep valleys have been cut by the streams into the original high plain, forming in many places very rugged hills. The relief is much less, however, than in the mountainous regions on either side. Some well developed oak-hickory woodlands occur; but the savannah type of vegetation is also common, *i.e.* scattered oaks or groves in grassland.

The Red River Region extends 170 miles along the southeastern border of the state. The greatest width is 45 miles but most of it is much narrower. Here the lower Cretaceous sands, shales, and limestones have weathered into deep, fertile soils. Oak and pine forests are common in the eastern part while savannah occurs in the west. Owing to the fertility of the soil and favorable moisture relations much of the land is under cultivation.

The Prairie-plains Region extends as a long, narrow tongue 150 miles southward from Kansas. It lies west of the Ozarks and extends far across the Arkansas River Valley. Throughout most of its length it ranges in width from 30 to 60 miles. Broad valleys and rolling hills with escarpments facing the east characterize this area. The underlying Pennsylvanian limestones and shales have weathered into fine-textured soils which under the existing climate are better suited to the development of grasses than forests. Since moisture is abundant, tall grass is the predominating type of vegetation.

The Sandstone Hills form an extensive region which lies west of the prairie-plains and Lower Arkansas Valley. It is about 50 miles wide and extends 180 miles southward from the northern border of the state. The Pennsylvanian shales have weathered, leaving rough, rather low hills of the more resistant sandstone. The maximum height of the hills is from 300 to 400 feet above the plain, although the average is much less. Much of the area is covered with a scrubby, transitional, oak forest but grassy areas are abundant. This region constitutes a large part of the savannah.

The Arbuckle Mountains, in the south-central part of the state, occupy a small area of about 860 square miles. They lie south of the sandstone hills and just west of the Ouachita Mountains from which they are detached. Here sedimentary, paleozoic rocks surround a central core of granites and other precambrian rocks. It is of the nature of a plateau which varies in elevation from 750 feet in the east to 1,350 feet in the west. It has been considerably eroded and many steep, rocky hills have been carved from the bedrock. The highest of these peaks are only about 400 feet above the valley floor but the topography is quite rough. The slopes and valleys are mostly forest-covered but grasses predominate on the upland.

The Redbed Plains, which traverse the entire state from north to south, form the most extensive region. The red Permian clays and shales have weathered into a gently rolling plain in which the hills seldom exceed 100 feet in height. The soils are for the most part fine and well suited to the

growth of grasses which dominate the region. Much of this area has been broken for agricultural purposes, the amount of native prairie increasing from east to west as grazing becomes more important.

The small Wichita Mountain Region lies within the southern part of the Redbeds in the southwestern portion of the state. The area is characterized by ranges of rugged and more or less barren peaks of granite which reach maximum elevations of 700 to 900 feet above the level of the Redbeds. The general level of the Redbeds is here about 1,100 feet above sea level and the maximum elevation of the peaks is approximately only 2,000 feet. Most of the mountains consist of great granitic masses almost destitute of vegetation above, but with a scrubby growth of oaks on the lower slopes. Between the peaks, the Redbeds are grass-covered. Most of the area has been set aside as the Wichita National Forest and is in its native condition except that much of it has been heavily grazed.

The Gypsum Hills constitute an extensive, rather irregular area extending across the state just west of the Redbeds. This is more or less sharply delimited from the Redbeds by escarpments which are especially steep both in the southwest and northwest. The greatest relief is found in the northwest where escarpments 200 to 400 feet high and narrow canyons of similar depth occur. In the central part of the state, the Gypsum Hills are more rounded and canyons and steep escarpments are less common. The relief increases again somewhat to the south. The soils are mostly fine-textured and hence of good water-holding capacity and quite fertile. The decreasing water content prevents a vigorous growth of tall grasses but enables the short, drought-resistant species to secure a foothold in the drier places. This results in a mixed prairie.

The High Plains occupy most of the "panhandle" and a small part of the northwestern portion of the state. The fine-textured soils are fertile but their water content is only sufficient to support a short-grass cover. This high, nearly level plain is interrupted by canyon-like stream courses and irregularly distributed tertiary sands, clays, and gravels. Where the soils are open, some tall grasses occur. The shrubby, rank-scented sumac and a few willows and cottonwoods are sparsely scattered along the streams.

DRAINAGE

The longer streams enter the state from the west in rather deep, narrow valleys and follow somewhat tortuous courses, crossing the state in an easterly or southeasterly direction. The principal drainage systems are those of the Arkansas and the Red Rivers. The Arkansas River System drains somewhat more than the northern half of the area (Fig. 1). The main stream enters the state from Kansas east of the center of the northern boundary and flows southeastward forming a broad valley between the Ozark and Ouachita Mountains. Its major tributaries, the Salt Fork, the Cimarron,

and the North and South Canadian Rivers drain the western and central parts of the state and follow somewhat parallel, southeastern courses. The Poteau from the south and the Verdegris, Grand, and Illinois from the north are its important tributaries in eastern Oklahoma.

The Red River System drains the southern portion of the state, of which it forms the southern boundary. It has a number of important tributaries. The Kiamichi and Little Rivers are short streams draining the southeastern portion. The Washita, flowing somewhat parallel to the Canadian, and the North Fork of the Red River in western Oklahoma, are the most important tributaries.

The rivers may be placed into three groups, each with rather distinct characteristics. The Grand, Illinois, Kiamichi, and Little Rivers drain the Ozark and the Ouachita areas and are beautiful, clear, mountain streams through most of their courses. Even when most turbid, they carry relatively little sediment. The Verdegris and Washita, on the other hand, are muddy streams; both arising and flowing through silt loam, consequently they do not carry much sand. Quite in contrast are the Salt Fork, the Cimarron, the North and the South Canadian, and the North Fork of the Red River as well as the Arkansas and Red Rivers themselves which are red, turbid, sand-laden streams. All follow relatively narrow, meandering channels through broad sand-choked valleys. They have their head waters in the Rocky Mountains, except the North Fork of the Red River, and are consequently subject to great seasonal fluctuations resulting from heavy rains and melting snow.

Disastrous floods are frequent; banks of water several feet high may rush down the valleys bearing enormous quantities of red clay, silt, and sand. These floods may continue many days, notwithstanding the fact that the streams flow for hundreds of miles through arid and semiarid regions before reaching the moderately level country near their mouths. Hence during these floods they usually receive little water from tributaries along their courses. When the high waters recede, the streams are characteristically small, winding rivulets in nearly dry channels. They may even dry up entirely leaving the materials of the extensive sand-bars at the mercy of the wind. Sand deposits, originally from near the source of the streams but now shifted various distances downward by the torrents, are blown into dunes by the prevailing southwest winds. The dunes are abundant within the channels and on the north banks. During recent geological times, sand deposits have spread themselves outward to a distance of 2 to 10 miles or more along the north sides of the streams. These sand dunes are now stationary and for the most part covered with vegetation although several small areas of actively moving dunes still remain. Sand dunes are extensive in western Oklahoma and also occur along the Cimarron and Salt Fork Rivers in the central portion, but are not found in the eastern third of the state.

General Plant Distribution

Two plant formations are present in Oklahoma. The Deciduous Forest *(Acer-Fagus)* Formation here reaches its western limit and the state includes three of the associations of the Grassland *(Stipa-Bouteloua)* Formation, *viz.*, true prairie, mixed prairie, and short-grass plains. The deciduous forest is present only in the eastern part of the state and along streams farther west where it extends into the grassland. It is represented by a single association, *viz.*, the oak-hickory *(Quercus-Hicoria)* forest. This association occupies

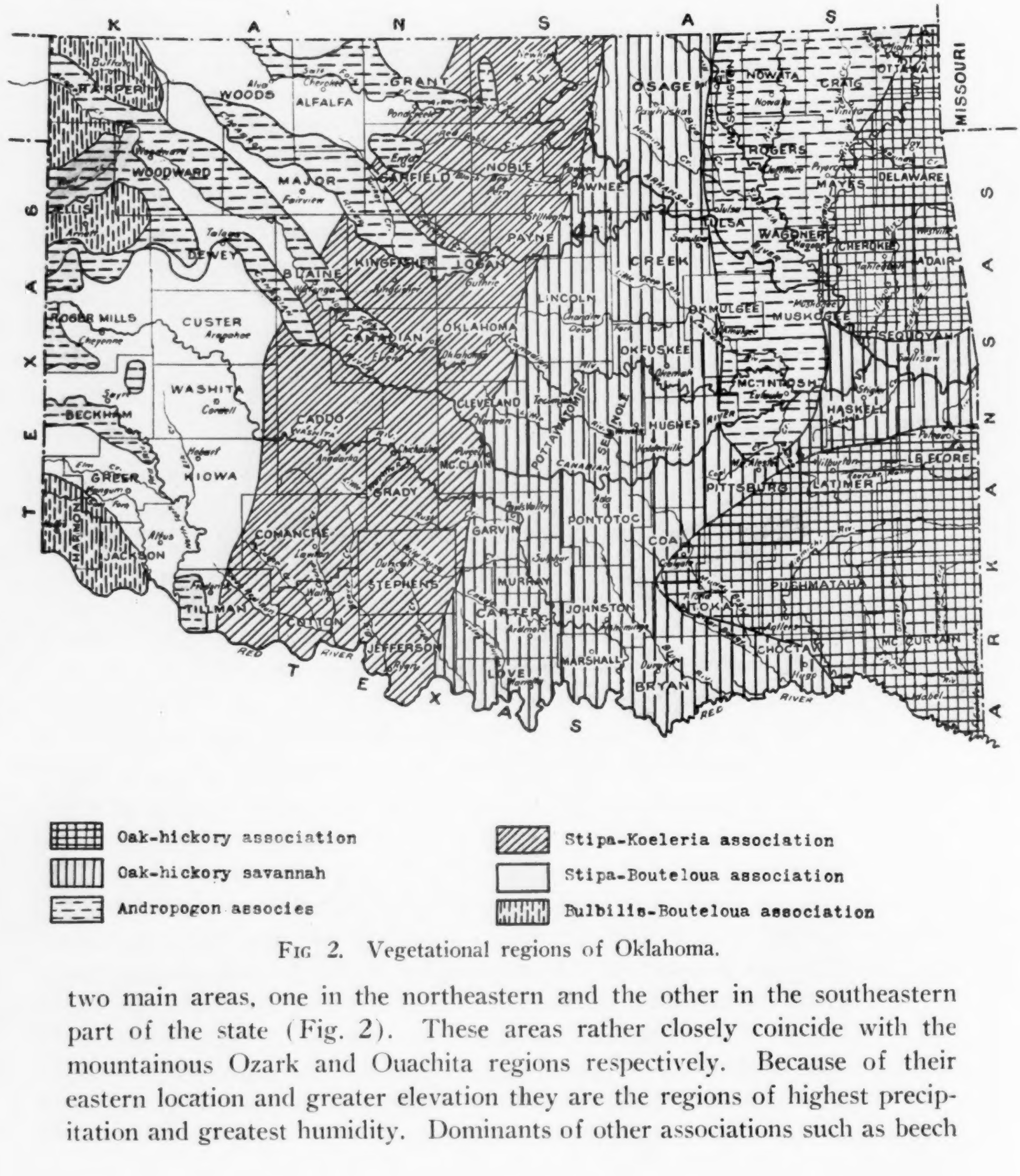

Fig 2. Vegetational regions of Oklahoma.

two main areas, one in the northeastern and the other in the southeastern part of the state (Fig. 2). These areas rather closely coincide with the mountainous Ozark and Ouachita regions respectively. Because of their eastern location and greater elevation they are the regions of highest precipitation and greatest humidity. Dominants of other associations such as beech

(Fagus grandifolia), hard maple *(Acer saccharum)*, linden *(Tilia americana)*, chestnut *(Castanea ozarkensis)*, etc., occur but not in the abundance or great stature which characterizes them in the still more mesic forests lying eastward. Moreover, they clearly show by their occurrence only in the most favorable sites that they are growing near the limit of their ranges.

The following oaks are common or abundant: *Quercus schneckii, Q. nigra, Q. velutina, Q. rubra, Q. marilandica*, and *Q. stellata*. The last two dominate only in dry situations. Associated with the oaks but of lesser abundance are various hickories, most important of which are *Hicoria ovata, H. laciniosa, H. cordiformis, H. myristicaeformis*, and *H. buckleyi*. These constitute a rather constant and variable but usually small percentage of the stand.

There are three other forest communities which bear a definite relationship to the climax deciduous forest. These are the subclimax shortleaf pine *(Pinus echinata)* consocies; the postclimax associes of blackjack and post oaks *(Quercus marilandica* and *Q. stellata)* intermixed with hickory *(Hicoria buckleyi)* which occupies the sandy uplands; and the flood-plain forest of elms and ash *(Ulmus-Fraxinus)* associes which extends far into the grassland climax.

The *Pinus echinata* consocies covers small areas in the extreme southeast. This community represents the northwestern extension of the southern pine forest. Pure pine forests occupy the poorer, rocky or sandy soils but such forests are of limited extent. On the more fertile soils they are intermixed with varying amounts of oaks and hickories, which will eventually replace them as soil formation and development of vegetation progresses. In fact, limited tracts of pine still occupy small areas throughout the Ouachita Region and are also found in the Ozark Mountains. Because of the rough topography and the consequent irregularity in the development of soil, it would require a detailed survey and a large scale map to represent accurately even the main bodies of these evergreen forests.

An extensive oak-hickory savannah (Fig. 2) separates the two climax forest areas and, except for the subclimax prairie, occupies the territory westward to the central portion of the state. This area is characterized by varying degrees of dominance of woodland and grassland. It is essentially a transition community between forest and prairie but its extent and character are controlled by the sandy texture of the soil. It is therefore a well defined edaphic community characterized by a definite floristic complex. In the northern portion, especially north of the Arkansas River where the soils are less sandy, grasslands predominate. This soil and grassland relation holds also for the broad southern part of the area including approximately the southern half of the territory lying between the Canadian and Red Rivers. In the remainder of the area, the soils are more sandy and a transitional type of oak-hickory forest predominates. The dominants are *Quercus marilandica*

and *Q. stellata.* These occur in about equal numbers. Constantly associated with these but of much less importance is *Hicoria buckleyi.* The grasslands associated with the forests of the savannah, range from subclimax in the eastern part to true prairie in the west.

The flood-plain forest, with its developmental stages, stands out as a distinct community not only in the grassland but also in the savannah woodland, where it sharply contrasts with the prevailing scrubby oak forests. In the climax forest region it forms a distinct developmental unit. In the east, the flood plains are dominated by willows, cottonwood, walnut, hackberry, honey locust, Kentucky coffee tree, etc. Various smaller trees, such as the ironwood and glossy-leaved Christmas holly and numerous shrubs, vines, and herbs abound. Among these, huckleberries, smilax, bittersweet, moonseed, may apple, and wood sorrel are representative. Westward both the number of species and successional stages diminish as increasing aridity limits the range of the more mesic plants.

The grasslands lie in the western half of the state except for a narrow tongue entering from the northeast. The eastern grassland is subclimax since it occurs in an area with a potential forest climate. The dominants are coarse, tall, sod-forming grasses such as various species of *Andropogon*, *Panicum virgatum*, and *Elymus canadensis*. Because of the recurrence of prairie fires, forest has not developed, but there is abundant evidence that forests are replacing the prairie since the settlement of the country and the cessation of fires. The western climax grassland is also interrupted by long bands of a similar type of prairie which occupies the sandy soils near the principal streams. This also includes sandy areas not definitely associated with the rivers. The tall, coarse, deeply rooted grasses characteristic of the subclimax prairie can occur in a prairie-plains climate because of the sandy substratum which readily absorbs all of the precipitation and permits it to penetrate deeply and at the same time forms a natural surface mulch which greatly inhibits evaporation. Thus this grassland, which extends far beyond its normal climatic limit, is clearly postclimax. There are also islands of savannah woodland, *i.e.*, oaks with a small percentage of hickory, which occur in the grassland west of the general savannah area. These are almost invariably found on local areas of sandstone or other types of rocky or sandy soil. They decrease rapidly in size and number westward.

The true prairie *(Stipa-Koeleria)* association lies to the west of the savannah. The chief dominants are species of *Andropogon*, *Bouteloua racemosa*, *Agropyron smithii*, and *Sporobolus asper.* Hosts of legumes, composites, evening primroses, etc., abound in the sod formed by the tall grasses. The relative scarcity of *Stipa* and *Koeleria* and the abundance of the andropogons may be explained in part on the basis of their origins which are from widely separated localities. The former species are of northern extraction but the andropogons are of southern origin (Clements, Weaver, and Hanson, 1929).

Thus *Stipa* and *Koeleria*, which are abundant in Nebraska and northward, become less so southward where the andropogons form consociations. Overgrazing has also played an important part in diminishing the amount of *Stipa* and *Koeleria*.

The mixed prairie *(Stipa-Bouteloua)* association is dominated by a mixture of tall and short grasses. The shorter andropogons, *viz.*, *Andropogon scoparius* and *A. saccharoides*, are the chief tall grasses along with *Agropyron* and *Bouteloua racemosa*. The short-grass dominants are *Bouteloua gracilis, B. hirsuta*, and *Bulbilis dactyloides*. This association has contacts on the eastern border with the true prairie and on the west with the short-grass plains. The soils have, characteristically, a lower water content due to the decreasing precipitation. Dry periods of long duration are more frequent and xerophytism is still further increased by the desiccating winds. Under these conditions of increasing aridity, the short grasses have an advantage over the tall ones, especially in the drier situations. Hence the area is characterized by extensive alternes and mixtures of tall and short grasses. Of the common grasses in the mixed prairie region, *Agropyron* is of northern origin while *Bulbilis* and *Bouteloua* have migrated north and eastward from the high plains of the southwest.

The short-grass plains *(Bulbilis-Bouteloua)* association occupies the extreme western portion of the state. It is characterized by an almost pure growth of the short grasses, enumerated for mixed prairie, which form a low sod-mat and constitute the most xeric type of vegetation. The water content of the soil is frequently very low due to the limited and unevenly distributed precipitation. The fine textured soil is capable of holding much moisture but the torrential rains seldom wet it below a depth of 20 to 25 inches, as is indicated by a hardpan at that depth. After rains much water is rapidly lost from the soil surface by evaporation due to strong, drying winds. The short grasses are capable of quickly reviving after a period of drought and are remarkably adapted to the conditions imposed by this environment.

GENERAL ENVIRONMENT

The environment of a plant consists of an intricate system of climatic and edaphic factors which exert profound influences upon it. Moreover, the factors themselves are greatly modified by the presence of vegetation. Oklahoma has a temperate climate which is subject to the extreme fluctuations characteristic of interior, continental areas. Its considerable width, great length, and difference in altitude afford a wide range of climatic conditions. As indicated by the vegetation, it has a temperate climate which is associated with deciduous forest in the east, prairie in the central part, and dry plains in the extreme west.

PRECIPITATION

The most important environmental factor in the latitude of Oklahoma is precipitation. The distribution of the various plant formations and associations depends in the main upon this climatic factor. The annual average precipitation ranges from 45 inches in the southeast corner of the state to 25 inches along the general western border but decreases to only 15 inches in the extreme western portion of the "panhandle." The effect of altitude is shown in the Ouachita and the Ozark regions where rainfall is 40 to 45 inches, while between them at the same longitude in the valley of the Arkansas

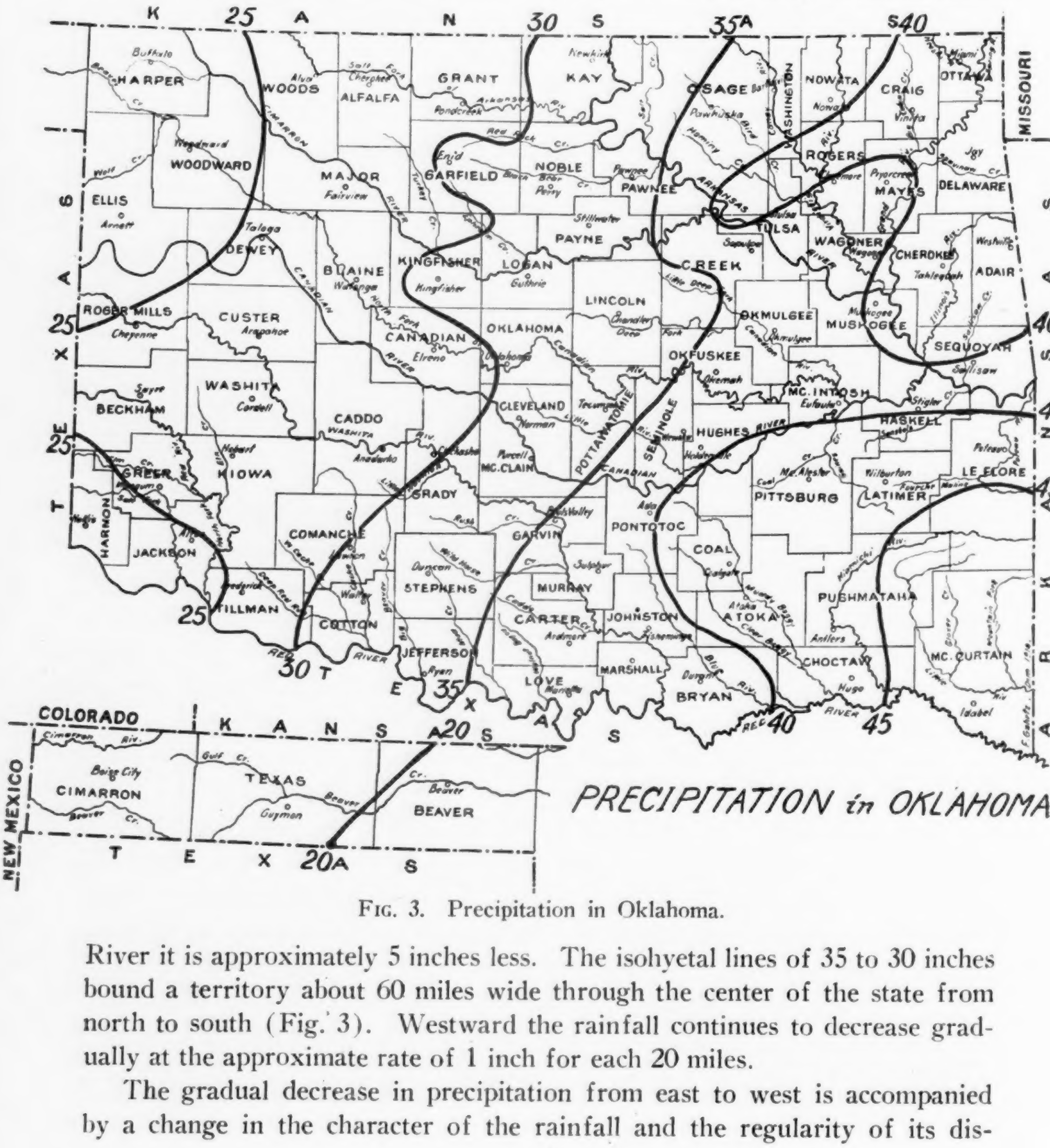

FIG. 3. Precipitation in Oklahoma.

River it is approximately 5 inches less. The isohyetal lines of 35 to 30 inches bound a territory about 60 miles wide through the center of the state from north to south (Fig. 3). Westward the rainfall continues to decrease gradually at the approximate rate of 1 inch for each 20 miles.

The gradual decrease in precipitation from east to west is accompanied by a change in the character of the rainfall and the regularity of its dis-

tribution throughout the seasons. Rains with a duration of several days are common in the east and long continued droughts are infrequent there. Both

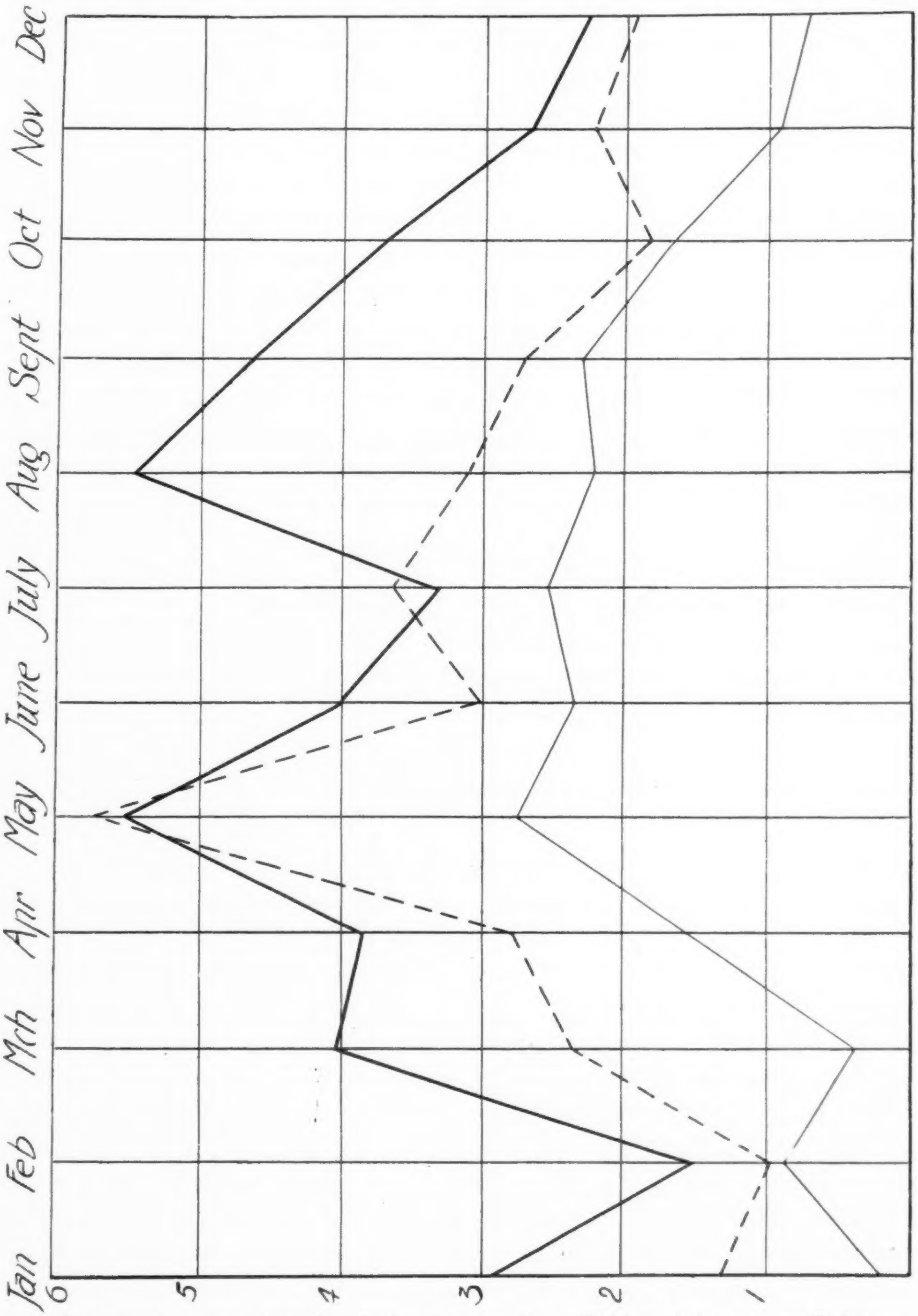

FIG. 4. Average rainfall in inches by months at Tahlequah in eastern Oklahoma (heavy line); at Oklahoma City in the central part of the state (broken line); and at Hooker in the west (light line).

soil and subsoil are thus thoroughly moistened. Westward there is a tendency for rains to become more and more torrential in nature and the showers are more irregularly distributed. This results in high run-off. Frequently 25 per cent or more of the rainfall is of no value for increasing soil moisture. The soil is seldom if ever moist below a depth of two feet and the water available for plant growth is nearly always exhausted before the end of the growing season. Moreover, all of the moisture from light showers and much of that falling in heavier rains is intercepted by the vegetation and evaporates again without adding to the supply available for absorption. Figure 4 shows the average monthly precipitation at Tahlequah, which is in the climax forest region of eastern Oklahoma, at Oklahoma City in the true prairie, and at Hooker which is in the short-grass plains. Tahlequah has two months, May and August, of maximum precipitation when the rainfall exceeds five inches. There is a long, moist growing season extending from March to October during which the monthly average is nearly four inches. At Oklahoma City there is only one month (May) when the rainfall exceeds four inches, and April to September is the time of greatest precipitation. At Hooker, where the moist season lasts only from May to September, there is about 2.5 inches rainfall per month. Thus, the length of the moist season decreases from 8 months in the east to 5 in the west, and the total amount of precipitation decreases about one-half.

The change in the character of the warm season precipitation is shown even more clearly by the number of periods of drought during which only .25 inch or less precipitation occurred in 24 hours. During the 20-year period, 1895-1914, western Oklahoma had an average of three droughts of 20 days duration during each growing season but such drought periods occurred only twice in eastern Oklahoma. Moreover, two of the three droughts were prolonged to 30 days in the west; where also drought periods of a duration of 70 days or more occurred on three occasions. Such droughts extended even as far east as Oklahoma City. Central Oklahoma is thus also subject to great extremes (Kincer, 1922).

In Oklahoma a large part of the rain falls during the growing season, April to September inclusive. This is distinctly advantageous to plants in a region of meager precipitation. The forested areas of eastern Oklahoma, for example, receive 24 to 27 inches of the total 40 to 45 inches during summer. The savannah has a rainfall of 21 to 24 inches and the prairie region 18 to 21 inches. The driest part of the state receives 15 inches or more of summer rainfall except in the western portion of the "panhandle" where it is somewhat lower. During winter little precipitation occurs anywhere in the state, even the forested portion receiving but 6 to 8 inches. The savannah region has but 4 to 6 inches, and only 2 to 4 inches fall in the grassland.

Soils

The types of bedrock in different parts of the state together with the varying climate and topography have resulted in the formation of many kinds of soil. Soil surveys, however, are available for only a very few counties and no comprehensive study has been made of the soil types, hence only general statements can be given.

The soils of the Ozark Mountains are rich and fertile on the level uplands and in the narrow valleys. Extensive tracts of flat, upland areas with moderately deep soil occur. In other places the soil is thinner and rocky. Over the area as a whole it consists of a fine textured, light colored, fertile, calcareous loam on which woodland is the natural climax. On the mountain slopes there is usually a cover of coarse, resistant chert fragments which remains intact long after the outcropping limestone has disintegrated. As a result, the slopes are very rocky with little or no surface soil although a sufficient amount of fertile soil occurs in the rock-crevices to support a good growth of forest trees. The sedimentary soils of the valleys constitute only a small part of the area but, though usually somewhat rocky, they are very fertile.

The soils of the Ouachita Mountains are for the most part neither deep nor fertile, but are thin and poorly drained. The mountains have little soil on the slopes due to the resistant nature of the Jackfork sandstone which, with certain other resistant rocks, constitutes the ridges. The fine textured soils of the valleys, which have resulted for the most part from the disintegration of shales, are usually poorly drained. The nature of the forest cover throughout the area is largely determined by the depth and fertility of the soil, which accounts for the variation in the character of the vegetation on the mountain slopes.

The subclimax prairie has soils which have been formed by the disintegration of limestones and shales in the north but in the south sandstones also have contributed to their formation. Hence, some rather coarse textured soils occur, but the fine textured, fertile loam that has originated from the shales and limestones predominates. The water-holding capacity is high (about 60 per cent by the Hilgard method) and the ample rainfall results in the high water content which is required to support the tall grasses of the region. In fact, the water relations of these grasses have been so carefully worked out that their presence may be taken as safely indicative of a high water content (Clements and Weaver, 1924). The greater part of the area is covered by tall grasses but where resistant bedrocks outcrop areas of woodland occur.

The savannah occupies the Sandstone Hills, the Arkansas Valley region, and extends into the Red River region. The soils are coarse textured, sandy, and relatively sterile throughout the central part of the state. They have a

low water-holding capacity and are occupied predominantly by the savannah woodland. Northward, near the Kansas line, and again in the south there are considerable areas of finer textured soils which are occupied entirely by grasses. These areas form extensive alternes with the woodlands of the savannah. Eastward, in the Arkansas Valley region, some fertile sedimentary soils occur in the valleys but much of the area is very rough on account of the outcropping Savannah sandstone and the Boggy sandstone formations. These fertile areas are covered with a scrubby growth of oaks. On some of the level areas in this region where the underlying rock is shale, such as the Atoka formation, the soils are fine textured and support a grassy cover. The Arbuckle Mountains, which are also included in the savannah, have soils which are mostly low in fertility and usually very shallow. The soils of the uplands are fine textured and frequently underlaid by bedrock at a depth of only a few inches. Little soil has accumulated on the rocky slopes but in the valleys some rich alluvial soil occurs. The vegetation of the region varies more or less with the soils. Grasses dominate on the uplands but on the slopes and in the valleys woody vegetation is characteristic. Thus, in general throughout the savannah, rocky outcrops and sandy areas are characterized by woodland while the finer textured soils are occupied by grasses.

Westward from the savannah the fine-textured soils of the grasslands have been formed from thick layers of clay, soft red shales, and thin layers of sandstone. These basic materials have developed the deep, fine-textured, red soils characterizing the Redbeds. These soils have a high water-holding capacity (about 60 per cent), which, in addition to their depth and fertility and the gently rolling topography, has led to the destruction of most of the native prairie for agricultural purposes. The soils of the gypsum hills farther westward are similar in nature and origin to those of the Redbeds except for the fact that ledges of gypsum produce rugged areas resulting in the formation of a certain percentage of untillable land. The level areas have fertile soils which are deep except near the gypsum outcrops. The water content of the soils in the gypsum hills is lower than in the Redbeds due to decreased precipitation, but the texture and fertility is similar in both areas. The increasing aridity has led to the preservation of a greater percentage of the native vegetation. The water relations are indicated by true prairie in the east and mixed prairie in the west.

From central Oklahoma westward, three soil belts occur in this Great Plains area according to Marbut (1923). All are characterized by the presence, on some horizon of the soil section or profile, of a zone of alkaline salt accumulation (usually, but not exclusively, of calcium carbonate) and a relatively dark colored surface soil. All these Great Plains soils, except those in the western two-thirds of the "panhandle" belong to the North Texas Division of the Black Belt. The surface 10 inches consists of a dark brown loam with a reddish shade; from 10 to 18 inches there is a granular, reddish

brown clay loam; and this is underlaid with a pinkish, highly calcareous clay. In the central "panhandle," the soil becomes lighter in color and the leached carbonates and alluviated clay under the decreased rainfall form a hardpan nearer the surface (Weaver and Crist, 1922).

The depth of the hardpan corresponds to the usual depth of water penetration and although usually only 12 to 18 inches deep, in the drier areas it may occur nearer the soil surface. Had it not been for the dense cover of short grasses which compacted the soil and by vigorous absorption prevented deeper water penetration, the hardpan probably would not have been formed. Because of the shallow water penetration, the soil is poorly adapted for the coarser and deeply rooted tall grasses. Thus the deep, fine-textured soils of the short-grass plains, notwithstanding their high fertility and great water-holding capacity once the water penetrates into them, support only a cover of short grasses. The water content is frequently reduced, as a result of the low precipitation, great run-off and high evaporation, to a point below that available for plant growth. Hence only the short grasses thrive, since they can endure the frequent recurrence of extreme drought. This is possible because of their low growth-form, low water requirement, and finely divided root systems which thoroughly ramify the soil. When water is available it is usually confined to the layer above the hardpan but occasionally the hardpan is moistened as the water penetrates more deeply. At such times roots also penetrate deeply but the scarcity of deep-rooted perennial herbs on the plains is doubtless explained by the fact that the grasses nearly always use the entire available water supply.

The sedimentary soils of the flood plains and terraces of the streams and the sandy areas deserve especial mention. The soils in the valleys of the large streams and their tributaries constitute a widely distributed system of the most fertile and productive lands of the state. The extensive sandy areas of central and western Oklahoma are for the most part also associated with the streams. They have been derived from the enormous quantities of sand deposited by the rivers which are unable to carry their load when not in a stage of flood and which are dry or nearly dry for a considerable period each year. During the dry periods the sand has been blown out of the river beds and heaped upon the adjacent plains.

WATER CONTENT

For the purpose of measuring and comparing water content of soil and other environmental factors, three stations were selected near Norman, in central Oklahoma, where the writer was in residence at the University of Oklahoma. One station was located in a large tract of grassland which was representative of the true prairie association. A second station was located in the savannah woodland community in which *Quercus marilandica* and *Q. stellata* were dominant. A third station was located in the postclimax forest

on the flood plain of the South Canadian River where the vegetation was in the late stages of development of the *Salix-Populus* associes.

The station in the true prairie occupied a gentle southeast slope centrally located in a half-section of grassland which covered a gently rolling plain. The soil was a clay loam underlaid at a depth of about four feet with a somewhat sandy substratum. It was reddish throughout except for the surface six to eight inches which, because of the presence of considerable humus, was nearly black. The soil was hard when dry but soft and plastic when wet. These properties caused it to erode easily. As indicated by plant growth, it was of only moderate fertility. Because of the compact structure and the dense cover of sod, run-off was high especially during torrential rains. When thoroughly wetted, after continued rainy weather, it held about 60 per cent of its dry weight of water and afforded a sufficient supply to the vegetation throughout long periods of drought.

The savannah woodland station was located about three miles east of the prairie. Between the two stations a sharp transition occurs. The silt loam covered with grassland gives way abruptly to a very sandy soil formed by the weathering away of an outcrop of Permian sandstone, which is continuous with the Sandstone Hills a short distance to the east. The soil, which varied from only a few inches to several feet in depth, was covered principally with blackjack *(Quercus marilandica)* and post oak *(Q. stellata)*. The instruments were placed on a gentle southeast slope under the forest cover.

The soil was a rather sterile, reddish sand. Approximately only the surface six inches contained humus in sufficient quantity to give it a dark color. From 6 to 36 inches there occurred a red sand which was quite powdery when dry. At greater depths poorly disintegrated sandstone covered the underlying bedrock. Water readily penetrated the soil and even during torrential rains there was little or no run-off. Only a small portion, however, was held in the coarse-grained soil; much of it rapidly percolated downward as gravitational water and drained away into the crevices of the underlying sandstone.

The flood-plain station was located in the broad sand-choked valley of the South Canadian River just high enough to be safe from the usual floods in times of high water. The soil to a depth of about 2 feet was a coarse-textured sandy loam which was evidently an old sand-bar. At greater depths it was less sandy and black in color and the proportion of silt and clay greatly increased. The water-holding capacity was therefore much greater at the deeper levels. Thus, during heavy rains absorption was great and the heavier subsoil was slowly saturated. All of the precipitation was retained in this manner except during very heavy and continuous rainfall.

TABLE I. *Water content in excess of the hygroscopic coefficient in 1924*

Date	Prairie				Savannah Woodland			
	0-6″	6-12″	1-2′	2-3′	0-6″	6-12″	1-2′	2-3′
April 5	21.0	24.0	15.0	17.0	12.2	16.8	12.0	13.3
" 12	11.2	24.5	13.2	12.1	11.1	6.6	9.3	10.5
" 19	7.6	12.6	10.7	8.6	8.9	7.2	7.2	10.7
" 26	24.0	19.2	14.1	16.3	13.5	13.4	15.3	14.6
May 3	17.2	14.5	12.5	17.1	12.1	12.4	13.6	14.1
" 10	11.1	12.4	4.7	9.7	11.9	11.2	16.0	16.2
" 17	4.7	5.6	13.7	9.1	9.0	7.0	10.1	15.1
" 24	2.0	3.5	9.6	6.5	5.2	9.5	5.2	9.5
" 31	2.3	5.9	9.3	6.4	5.6	10.4	19.7	16.8
June 7	5.6	4.8	9.1	7.5	8.6	6.1	6.0	4.4
" 14	3.7	2.7	8.8	4.8	5.3	4.8	3.9	2.2
" 21	2.6	2.0	5.3	4.3	2.3	2.8	1.9	1.0
" 28	1.2	1.1	8.3	4.2	0.8	0.7	0.2	0.1
July 5	2.2	1.8	6.4	4.5	2.0	1.4	0.1	0.1
" 12	2.3	0.8	4.4	5.1	3.8	2.7	2.1	1.6
" 19	1.3	1.9	2.3	2.8	0.3	0.9	3.9	1.7
" 26	0.7	2.1	1.6	1.4	0.1	0.1	1.7	0.5
August 2	2.3	2.1	1.6	0.6	0.1	0.2	0.4	0.4
Hygro. Coef.	6.9	9.2	11.8	11.0	1.8	1.2	0.9	1.5

Table I shows the water content at the prairie and savannah woodland stations in excess of the hygroscopic coefficient which is approximately the water available for growth (Alway, 1919; Weaver, 1920). The hygroscopic coefficients are also given for the several depths of the different soils. The clay soils of the prairie have a relatively high hygroscopic coefficient but this is very low in the coarse-textured sands of the savannah woodland. As a result, the total water content and frequently the water content in excess of the hygroscopic coefficient are greater at any given time for the prairie soils.

The available water is relatively high for both stations in the early part of the growing season, *e.g.* early in April. It did not become unfavorably dry until after the middle of May when water content was reduced to 2 or 3 per cent in the loam soil. Thereafter the supply steadily diminished and late in

June and during July and August little or no water was available for growth in the first foot of soil. In August, little or none remained in the second and third foot.

Table II. *Water content in excess of the hygroscopic coefficient in 1925*

Date	Prairie					Savannah Woodland			
	0-6″	6-12″	1-2′	2-3′	3-4′	0-6″	6-12″	1-2′	2-3′
April 8	6.7	6.0	5.5	5.3	11.2	10.3	12.0	2.7	1.1
" 15	10.7	9.6	10.7	9.0	10.7	9.8	12.4	3.0	2.4
" 22	11.1	8.2	9.9	8.1	11.2	14.1	11.2	7.6	1.3
" 29	13.2	10.4	11.3	9.2	10.8	12.4	10.9	11.4	10.7
May 6	10.7	9.4	9.1	8.2	9.5	11.9	11.4	10.7	10.1
" 13	18.5	16.2	14.7	15.8	9.5	16.6	11.2	12.6	16.2
" 20	20.6	10.9	18.8	14.4	10.7	10.6	10.8	11.3	14.0
" 27	10.1	8.1	8.6	2.2	3.1	7.6	9.3	8.9	10.7
June 3	10.1	9.0	10.7	11.6	10.7	6.8	8.4	6.8	8.9
" 10	6.9	9.2	11.8	11.0	10.1	10.1	10.5	5.9	7.0
" 17	5.9	8.7	10.8	10.7	9.3	7.2	8.1	4.3	5.1
" 24	4.3	6.5	8.4	9.6	9.3	4.0	3.7	2.1	4.0
July 1	2.1	4.0	5.3	5.3	7.9	1.0	2.3	1.0	2.0
" 8	1.4	2.1	2.0	3.0	6.9	0.8	0.5	0.1	0.3
" 15	1.3	0.9	1.9	0.7	6.2	0.2	0.6	0.1	0.1
" 22	0.1	1.0	1.1	2.3	2.9	0.1	1.0	1.1	2.3
" 29	22.1	16.3	5.2	2.1	2.0	10.4	12.3	11.7	8.5
August 2	7.3	14.6	1.7	3.3	4.5	7.1	5.4	5.1	1.6
Hygro. Coef.......	6.9	9.2	11.8	11.0	11.1	1.8	1.2	0.9	1.5

An examination of the table shows that on the coarse, sandy soils of the savannah woodland all but 1 or 2 per cent of the total water content was available to the plants. In the prairie, however, the hygroscopic coefficient varied from approximately 7 to 12 per cent. After a heavy rain, the soils at depths of 2 to 3 feet soon became wetted in the sand but in the more retentive loam soils of the prairie, percolation was very much slower. Owing to the mulch of dry sand in the savannah, little water was directly lost by surface evaporation. Hence, for all but a few determinations, more water was avail-

able in the surface six inches here than at the prairie station. In fact, no great differences were found between the amounts of available water at greater depths. This was possibly due in part to the fact that the grassland cover transpired water in an equal or greater amount than the woodland, and undoubtedly due to the loss of water through run-off in the grassland, a factor which was practically nil in the sandy soils.

The soil was moderately dry on April 8, 1925, but the water content increased rapidly as a result of spring rains (Table II). Early in June, it began to decrease and this continued until the last of July when a rain wet the surface 12 to 15 inches. Thus the early part of the growing season was characterized by a relatively large amount of available water at all stations. It ranged from 9 to 26 per cent in the flood plain, 8 to 24 per cent in the prairie, and 7 to 15 per cent in the savannah woodland. After the middle of May or the first of June there was a rapid decrease. This continued until there was practically no moisture available to a depth of four feet except on the flood plain where it never became deficient because of subirrigation. The soils were drier here in summer than in spring but water was always abundant.

Certain irregularities in the water content, especially in the deeper layers of soil, were due to factors other than precipitation. Impermeable layers of rock occurred within a few feet of the surface at the prairie station and bedrock was found at a depth of about five feet in the savannah woodland. Water seeping along these rocky layers sometimes subirrigated the soil for short periods. Numerous wet-weather springs are also common along the sides of ravines. They are characterized by a slow seepage rather than a flow of water.

HUMIDITY

The amount of water vapor in the air is one of the major factors influencing vegetation. It is of paramount importance since it directly affects the rate of transpiration. In fact, humidity frequently determines whether a plant can or can not grow in a given habitat. Consequently, it must be considered in all problems concerning the distribution of vegetation. Relative humidity is closely related to precipitation. There is a tendency throughout the grasslands for dry years to occur in cycles. Climax vegetation thrives best, of course, during the more moist years but it is also adapted to endure drought.

Since humidity varies rather directly with precipitation, the air becomes increasingly drier from the eastern to the western part of Oklahoma, that is, from the more mesic to the more xeric plant associations. Directly northward and southward there is little variation, the humidity of eastern Oklahoma being in general similar to that of eastern Kansas and western Missouri. Except for winterkilling, resulting from desiccation at low temperatures, which rarely occurs among native plants in Oklahoma, winter humidities are of minor importance. They range from less than 50 per cent in the extreme west to about 63 per cent (at 2 p. m. in January) in the extreme east. The average

relative humidity in midsummer afternoons (2 p. m. during July) is 40 per cent in the short-grass plains and about 53 in the deciduous forest. The average minimum humidity, however, falls to 35 per cent on the short-grass plains and about 48 per cent in forested areas in the east. Although the average varies from season to season, the same general relationship holds for the various portions of the state. The monthly average for each community for April was 5-10 per cent lower and for October 5-10 per cent higher than the July average (Kincer, 1922).

The humidity was measured by means of a cog psychrometer. Readings were made between two and four o'clock p. m. From many readings from April to August during a period of two years it was found that a much drier atmosphere surrounds the prairie vegetation than that of the woodland. During 1924 the humidity varied from 15 to 59 per cent in the prairie with an average of 40, but in the savannah woodland it fluctuated between 26 and 71 with an average of 58 per cent. The range in the prairie during 1925 was between 39 and 70 per cent with an average of 60; in the savannah woodland, the variation was from 51 to 79 per cent with an average of 67; and in the flood-plain forest 62 to 73 and an average of 69 per cent.

The lowest humidity in the prairie occurred during midsummer but in the woodlands it was lowest before the development of the foliage. The minimum difference between the habitats occurred on moist, cloudy days when the humidity was only 2 per cent lower in the prairie. The maximum difference occurred on dry, hot days when the humidity fell as low as 15 per cent in the prairie but was at no time less than 41 per cent in the woodland. No consistent variation was found between the two woodland stations. The maximum variation between them was only 8 per cent and the humidity was frequently the same in both.

Light

Oklahoma has much bright, clear weather. About 54 per cent of the days are cloudless, 25 per cent partly cloudy, and only 21 per cent cloudy. Since there is an abundance of sunshine, light becomes a critical factor in the development of the vegetation only in the ecotone between forest and grassland and in the woodland communities proper. The intolerant nature of the prairie grasses prevents their growth among shrubs or trees and in competition with other woodland plants.

Temperature

Temperature relations are as a whole favorable throughout the state for plant development. The average date of the last killing frost in the spring is March 21 in the southeast, while in the northwest it is one month later. The average date for the first killing frost in the fall is November 1 in the southeast and October 21 in the northwest. Throughout the central part of the state these dates are April 1 and November 1, respectively. Thus, there is a

growing season of 180 days in the northwest, 210 in the center, and 230 in the southeast. The hot, relatively dry summers are preceded by a long, balmy spring season and followed by many weeks of cool autumn weather. During winter zero temperatures occur only infrequently and temperatures below the freezing point are of short duration. The duration of the period with a normal daily mean temperature of 32° is 30 days along the northern border but this number rapidly diminishes southward to zero for the whole southern half of the state. The average monthly temperatures at stations in three widely separated plant communities are shown in Table III.

TABLE III. *Mean monthly temperatures in degrees Fahrenheit at Idabel in southeastern, Oklahoma City in central, and Hooker in northwestern Oklahoma.*

STATION	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
Idabel......	46	50	55	66	72	77	80	80	76	68	60	42	65
Oklahoma City.....	36	39	50	59	67	76	81	80	72	61	48	39	59
Hooker.....	33	36	46	55	63	74	78	77	70	56	44	34	56

There is a gradual decrease in temperature with the increase in altitude and latitude toward the northwest.

The average winter temperature for December to February is about 46° F. at Idabel but at Hooker it is below 35° F. (Kincer, 1922). Throughout most of the state the average lies between 35° and 40°. The average summer temperature (June-August) is 80° or more along the entire southern border but throughout the remainder of the state, except for Cimarron County, the average lies between 75° and 80°. The extreme northwest has fewer than 120 consecutive days with a normal daily mean temperature of 68°, in the southern part of the state the number exceeds 150, while the whole central portion lies between this range (Livingston and Shreve, 1921).

Air temperatures were secured by the use of Friez' thermographs placed in the field. The average weekly maximum temperature was secured by averaging the highest reading for each day of the week and the average weekly minimum temperature by averaging the lowest daily readings. The average day temperature was ascertained by adding the readings of the even hours from 8 a. m. to 6 p. m. and dividing by the total number of readings for the seven days of the week, and the average night temperatures by using the readings from 8 p. m. to 6 a. m. The average maximum and minimum temperatures give an idea of the extreme range through which the temperature fluctuates. They are important since plant distribution may be controlled by temperature extremes. The average day and night temperatures are likewise important since they show the average conditions of heat under which the plants grow.

Table IV. *Average air temperatures in the prairie and savannah woodland.*

1924	April		May					June				July				August
	19	26	3	10	17	24	31	7	14	21	28	5	12	19	26	2
Prairie																
Maximum	91.0	93.0	75.3	80.2	81.0	85.2	87.6	92.3	103.0	103.0	103.0	94.0	99.3	113.0	113.0	108.0
Day	72.2	74.3	65.0	77.2	65.0	70.8	71.9	77.2	91.5	95.0	93.4	85.4	88.5	99.3	101.2	99.2
Night	63.1	65.1	55.0	68.8	53.2	62.9	62.6	64.5	80.3	83.3	81.2	74.8	77.4	85.4	88.9	87.0
Minimum	53.0	49.1	48.2	44.5	45.1	56.0	50.3	56.5	73.4	75.2	76.0	64.3	68.9	78.2	75.1	74.0
Savannah Woodland																
Maximum	95.1	91.0	81.0	74.0	83.0	83.0	87.0	89.3	92.1	95.0	94.7	95.2	88.0	99.1	98.4	98.3
Day	68.8	78.0	68.2	71.7	69.7	67.8	64.1	71.6	85.4	88.6	88.2	74.1	78.9	86.2	86.2	88.6
Night	52.4	61.0	50.3	48.0	56.0	60.8	56.4	67.1	71.7	80.0	78.6	65.3	69.6	78.3	74.9	77.5
Minimum	36.0	47.0	43.7	35.7	48.2	43.5	57.8	55.3	70.1	70.0	74.1	57.2	57.5	70.4	61.9	66.7

1925	April				May				June				July				
	8	15	22	29	6	13	20	27	3	10	17	24	1	8	15	22	29
Prairie																	
Maximum	70.8	81.2	92.3	78.1	83.3	69.2	81.1	85.8	84.5	86.3	91.0	92.5	96.1	98.8	98.8	103.6	95.3
Day	65.9	74.2	87.4	73.2	76.4	64.7	76.5	80.2	80.1	82.2	85.4	86.5	86.6	91.2	94.2	97.0	90.3
Night	51.0	63.0	77.7	68.6	62.3	59.7	72.9	70.9	81.8	73.6	74.1	74.5	73.1	80.6	83.8	84.8	80.5
Minimum	49.8	59.4	70.1	64.8	58.5	52.0	65.1	66.5	69.4	69.8	70.5	70.6	67.0	79.8	80.1	79.6	78.5
Savannah Woodland																	
Maximum	65.7	86.3	90.9	72.7	81.0	64.8	70.3	80.8	84.3	86.5	87.0	90.6	90.5	88.5	92.4	94.1	90.5
Day	60.7	74.7	82.1	67.3	75.2	61.3	67.1	73.5	76.4	80.1	84.1	85.6	83.7	83.6	87.1	83.2	81.0
Night	49.7	56.1	74.0	59.5	60.8	58.5	61.3	65.5	68.7	72.4	75.5	75.8	69.8	76.3	77.5	77.4	73.7
Minimum	47.4	51.5	70.5	61.2	57.1	56.0	57.3	63.3	65.4	70.6	73.8	72.1	64.8	73.1	73.0	72.5	71.1

Table IV shows that temperatures were continually favorable for plant growth after the first of April and that very high temperatures sometimes occurred early in the season. Typically, there is a period of moderately warm weather during the spring and mean temperatures usually increase gradually, but high temperatures in summer often occur rather abruptly. During the third week in May of 1925, the average day temperature exceeded 80° F. When such high temperatures prevail and are associated with low humidities the grassland vegetation soon begins to dry and growth is materially checked until the occurrence of rains accompanied by lower temperatures. Estival plants mature but serotinal species show little activity during these extremely dry, hot periods.

A comparison of the temperature data for the two years shows that in early spring that of the grassland averages about the same or somewhat less than that of the savannah woodland. Lower temperatures occur in the forests when the leaves of the trees are fully developed. The extremes are greater and the average temperatures higher on the prairie on account of direct insolation.

Soil temperatures were also measured during a period of two years at depths of 6, 12, 18, 24, 36, and 42 inches respectively. Temperature at the 6-inch level varied from 68° to 107° F. in the prairie and 52° to 85° in the savannah woodland. At the 12-inch depth the range was 61° to 94° and 55° to 83° respectively. At greater depths the prairie soils were also warmer, except in early spring before leafing. At a depth of 4 feet, for example, the range was 60° to 78° in prairie and 57° to 69° in woodland. The prairie was screened from insolation only by the grass cover and in many places where this was sparse the soil received direct sunlight.

After the first of May the surface warmed very rapidly, and during June (1924) the soil temperature at a depth of 6 inches increased from 86° to 107° F. During the same period in the savannah woodland the temperature at the same depth increased from 71° to 78°. Due to the protection afforded by the forest canopy and leaf mold, the surface soil of the woodland did not reach its maximum temperature until the middle of July. A general upward trend in soil temperatures until the first of August was characteristic at all stations for both years. Temperature fluctuations at a depth of 6 inches closely followed the daily fluctuations in air temperature, although only a slight daily variation occurred at a depth of 18 inches. A rise of 2 or 3 degrees came nine hours later than the maximum air temperature and six hours later than the maximum soil temperature at the 6-inch level.

The high temperature and the great variations in temperature are important factors in grassland soil. The former causes a decrease in relative humidity and promotes more vigorous transpiration. Absorption is probably increased by a higher soil temperature. Under such conditions excessive water loss is promoted and woody species can not thrive.

Wind

Wind is an indirect but very important factor in plant habitats. It influences the water relations of plants both through its effect on transpiration and evaporation from the soil. Its mechanical action influences plant growth and its erosive action on the soil is often marked. The western part of the state is especially subjected to high winds and their impress on the few woody species that occur is shown by deformed and distorted crowns. Since the dry winds, which blow more or less constantly during the growing season, are prevailingly from the southwest, the crowns of trees and tall shrubs often develop more extensively on the north or leeward side. This is a response in part to mechanical action but largely to the greater desiccating effect and consequent poorer growth on the exposed side. The twisted cedars on rocky exposures and the flattened crowns of elms in the prairie region are examples of wind action. The general absence of broad-leaved woody plants and tall species of herbs is characteristic of dry, windy regions.

Quantitative measurements of wind action in erosion and deposition have not been made but the cumulative result is great. The almost continuous winds are always laden with material which is in process of transportation. For days, weeks, and even months at a time during periods of drought, insolation is greatly decreased and a haze prevails owing to the large amount of dust in the air. Throughout the Redbeds, in the High Plains to the west, and to a smaller degree in the sandstone soils of the savannah region, enormous quantities of loose soil are blown from cultivated fields, trampled pastures, and other unprotected areas. This may occur even on dry clay soils but sandy soils especially are subject to wind action and a few areas of active dunes occur within the state. Areas of drifting sand several hundred yards in length and often a hundred yards wide are frequent along streams as far east as central Oklahoma.

Evaporation

The rate of water loss from the soil by evaporation as well as the amount transpired by plants is modified by the cover of vegetation which influences temperature, relative humidity, and wind movement. The local effect of vegetation, however, is largely eliminated in measurements of evaporation from free water surfaces such as large open tanks. For purposes of general climatological comparison, however, such measurements are instructive. In western Oklahoma, 50 to 55 inches of evaporation occur from a free water surface during the six summer months. The high evaporation rate is due to relatively high temperatures, high and almost continuous winds, and low relative humidity. Tanks similarly located in western Nebraska gave an evaporation of 41 inches and in North Dakota only 31 inches. This great increase in evaporation southward causes the 20 inches of rainfall in the "panhandle" to be only as efficient as 15 inches in western North Dakota

(Briggs and Belz, 1911). Similarly, 20 inches precipitation in eastern North Dakota is equivalent to 25 inches in the western third of Oklahoma. Extensive observations made during the past 20 years show that evaporation varied from 37 to 52 inches at Lawton, in Comanche county, and from 42 to 58 inches at Woodward, in Woodward county (Chilcott, 1927).

TABLE V. *Evaporation in cubic centimeters from standardized, cylindrical cups at the prairie and savannah woodland stations.*

1924	Prairie	Savannah Woodland	1925	Prairie	Savannah Woodland
April 19	26.6	24.5	April 8	25.0	16.0
April 26	39.9	26.4	April 15	29.0	19.0
May 3	11.8	9.7	April 22	67.1	37.2
May 10	29.1	13.6	April 29	21.4	13.8
May 17	30.6	12.5	May 6	11.4	11.5
May 24	39.0	13.6	May 13	6.1	2.9
May 31	17.4	6.8	May 20	17.0	8.1
June 7	33.0	10.7	May 27	41.4	16.7
June 14	42.0	12.2	June 3	41.0	16.0
June 21	63.7	19.0	June 10	46.0	19.7
June 28	67.0	21.0	June 17	45.1	16.7
July 5	34.2	9.5	June 24	59.1	19.5
July 12	47.3	19.1	July 1	60.0	17.6
July 19	60.1	28.0	July 8	46.0	19.8
July 26	41.3	17.3	July 15	43.8	20.1
August 2	40.1	16.8	July 22	69.8	23.4
			July 29	42.0	15.9
			August 6	41.1	14.2

The average daily evaporation for each week was determined at the two stations by the use of Livingston's cylindrical, porous-cup atmometers of the non-absorbing type. Two standardized cups were operated in typical areas and the average losses are given in Table V. A gradual increase in evaporation from early spring until midsummer was determined although great variations resulted from transient differences in temperature, humidity, and wind velocity. The maximum daily evaporation on the prairie (70 cc.) occurred during the week of July 22, 1925. That of the woodland was recorded for the third week in April, 1925, just before the trees and shrubs were in full leaf. A

warm, dry, south wind of several days duration greatly increased water loss. The influence of the protecting cover of woodland is shown by the fact that the evaporation at this station was only 37 cc. as compared with 67 in the prairie during the same period.

Early Botanical Explorations

Information on the vegetation of Oklahoma secured by early explorers and traders is meager except in some cases where a biologist accompanied the party. Such records constitute the only source of information concerning conditions before the region was opened for settlement. Perhaps the earliest and most authentic record of the vegetation is found in Nuttall's Journal (1821) concerning the "Arkansa Territory," and in his report of collections which was read before the American Philosophical Society in 1834. Nuttall spent most of the summer of 1819 collecting plants and describing the vegetation. Entering the state in the region of the Arkansas River Valley in company with a small military expedition, his course took him across the Poteau River and through the Ouachita Mountains. After the party crossed the divide from the valley of the Poteau they followed more or less closely the course of the Kiamichi to the Red River. He forcefully portrays in his journal, not only the nature of the vegetation of the woodland and the strips of prairie encountered but also the plant life of aquatic habitats. Of the prairies of the savannah and the grassy openings of the forested areas he says: "These vast plains, beautiful almost as the fancied Elysium, were now enameled with numerous flowers, among the most splendid of which were the azure larkspur, gilded coreopides, fragrant phloxes, and the purple *Psilotria*. Serene and charming as the blissful regions of fancy, nothing here appeared to exist but what contributed to harmony." The "pathless thickets," the "sombre belts of timber" where "wooded hills prevailed on either hand" and the "rocky pine ridges" are all appropriately descriptive of the region.

Nuttall's next expedition was up the Arkansas River. He noted the decreasing stature of the woody vegetation and the increasing amount of prairie as he proceeded up stream past the Illinois and Grand Rivers. He also explored a portion of the Verdegris. Later, his explorations extended westward into the region of the Cimarron and Canadian River valleys. For the most part it lay through the savannah portion of the state. In addition to his field notes, an almost complete thermometric table accompanies his report. These early morning and mid-afternoon readings constitute the first temperature observations made in the state.

In 1820 Major S. H. Long traversed the state from west to east along the course of the South Canadian River. From his journal (1823), which was prepared by Edwin James, biologist and geologist of the expedition, a fairly good idea of the primaeval condition of the vegetation may be obtained.

Josiah Gregg, a Santa Fé trader, records in *Commerce of the Prairies* (1844) eight expeditions across the great western prairies. On two occasions he traversed the central part of the state along the course of the Canadian River. The more frequented trail, however, passed through the northwestern part. Although his description is of a general nature, the outstanding features of the vegetation are clearly set forth. The timbered portion of the United States Territory east of the "Cross Timbers" and the luxuriant eastern "interior" prairies are mentioned. "The Cross Timbers may be considered as the fringe of the great prairies. It is a continuous brushy strip composed of . . . blackjack, post oaks and in some places hickory, elm, etc., intermixed with a very diminutive oak." Prairie fires are assumed to be the main factor in keeping the more moist prairies free from trees and even at this early date pioneers had observed the spread of forests into various grassland areas which were protected from fire. He also mentions the decreasing stature of the woody vegetation and its scarcity westward. The gypsum hills and the great sandy plains are features which were early recorded. The great forage value of the "mesquite" and "grama grasses" and numerous common herbs, shrubs, and trees are also pointed out.

Sitgreaves and Woodruff, with S. W. Woodhouse as naturalist for the expedition, surveyed the northern boundary of the Creek Indian country in 1849 and 1850. The parallel 36° 8′ 42″ north was followed from the Verdegris nearly to the 99th meridian and the return was by way of the North Canadian River to Fort Gibson. The general features of the vegetation along the Arkansas, Neosho, Verdegris, and the North and South Canadian Rivers were indicated on a large scale map.

Captain R. B. Marcy in his exploration (1852) of the Red River of Louisiana gives a good description of the vegetation along the route traversed, especially the woody vegetation. The expedition started in Texas and entered Oklahoma in the vicinity of Cache creek, passed through the Wichita Mountains and the gypsum hills and proceeded westward. The report (1853) contains five drawings which seem to be the first views of the region. These convey an idea of the outstanding topographic and vegetational features of the Wichita Mountains and the gypsum hills. Nineteen full page plates show some of the characteristic plants. A list of the plants collected was prepared by Doctor John Torrey.

Bigelow (1856) gave a brief but excellent description of the vegetation of Oklahoma as it was observed in crossing the state from east to west. He described the land as "being in nearly its whole breadth a beautiful and fertile country" and includes a long list of trees, shrubs, and other plants encountered. The "Cross Timbers" and the alternating areas of prairie and woodland are described as being "most beautiful and picturesque" and arranged so as to "give them the appearance of vast cultivated fields formed on a scale of great magnitude stretching away in every direction as far as the eye can

reach." In the western portion he found grassy plains with timber present only along the streams. A report on the general botanical collection was prepared by Torrey (1853), the *Cactaceae* being identified by Engelmann and Bigelow (1856).

Later Investigations

Systematic lists of species have been given by Butler (1878) and Holzinger (1892). Carleton (1892) was the first to summarize his observations on the distribution of the vegetation in the state.

Fitch (1900) reported on the distribution of the woodlands throughout the greater portion of Indian Territory. The brief general description of the timber in each township, which was determined from surveyors' notes, is especially instructive. His is the only map showing the distribution of vegetation in detail in any part of the state.

Bogue (1900) published the first annotated catalogue of ferns and flowering plants. The plants of the Indian Territory were not included since sufficient information was not available to make this possible. Van Vleet (1902), using the plants in the herbarium of the Oklahoma Geological Survey, listed more than 800 species. The dates and localities are not given and this extensive collection was lost by fire before the catalogue was completed.

Gould (1903) made a list of the trees, shrubs, and vines of the Cherokee Nation. Shannon (1913), in his report on the trees and shrubs of Oklahoma, gave a rather complete list of the native and introduced species. Stevens and Shannon (1917) in a report on the plant life of Oklahoma, also gave a short general description of the vegetation and a systematic presentation of the species.

The ecological investigations in the Red River Valley by Tharp (1923) in connection with the Red River Boundary case deal with the vegetation of both Oklahoma and Texas. Palmer (1924) made an intensive study of the flora of Rich Mountain, one of the peaks of the Ouachitas. Hefley (1927) gave a preliminary report of the seasonal aspects of six habitats near Norman. Featherly (1928) lists the grasses of Oklahoma, and Ortenburger (1928) lists, in two papers, representative plants of typical communities in Oklahoma.

Some important papers dealing in part with the natural vegetation in connection with afforestation are those by Hall (1900, 1903), Clothier (1905), Alexander (1910), and Phillips (1926, 1927). Contributions by Buckley (1883), Rydberg (1901), and Sargent (1918) have done much towards clarifying the problem of the systematic relationships of the numerous species of oaks that are predominantly characteristic of large areas.

Deciduous Forest Formation

The deciduous forest formation occurs in eastern Oklahoma and is also represented along the streams westward. Numerous species which are dom-

inants of this formation in Missouri, Ohio, and eastward occur here only in protected areas or where conditions are especially mesic. Among these beech, maple, birch, red oak, linden, and ironwood are representative. Their occurrence in Oklahoma indicates a true relationship of this woodland with the eastern deciduous forests. Oaks and hickories dominate under conditions characteristic of the region as a whole. *Quercus alba, Q. phellos, Q. nigra, Q. schneckii, Q. rubra, Q. velutina, Q. marilandica,* and *Q. stellata* are the common oaks of the region. They are characteristically accompanied by various species of *Hicoria.*

There are four forest communities which bear a definite relationship to the climax deciduous forest. The *Quercus-Hicoria* association occupies the rough mountainous areas of the eastern part of the state. Within the boundary of this association the subclimax *Pinus* consocies occurs over limited areas. Westward, the oak-hickory savannah, characterized by *Quercus marilandica, Q. stellata,* and *Hicoria buckleyi,* forms a transitional and edaphic community. Along the streams there is a characteristic woodland which is different from the forest proper.

OAK-HICKORY *(Quercus-Hicoria)* ASSOCIATION

The climax oak-hickory forest occupies two more or less semicircular areas (Fig. 2). The smaller one lies in the northeastern portion of the state, where it enters from the east and is continuous with the deciduous forest of the central states. It centers in Delaware, Cherokee, and Adair counties, and includes the eastern portion of Mayes, northeastern Muskogee, and northern Sequoyah counties. A comparison of the physiographic and the vegetational maps (Figs. 1 and 2) shows that this area extends slightly beyond the Ozark region. This association gives way through a narrow transition to the subclimax prairie which lies to the north and west and merges with the oak savannah on the remainder of its western border. It is separated from a similar larger southern area by a strip of savannah which occupies the lower elevations with less rainfall in the vicinity of the Arkansas River.

The larger area of deciduous forest also enters from the east and occupies an extensive area in the southeast. It is the dominant formation in McCurtain, Pushmataha, and several adjacent counties. The forest occupies the Ouachita Mountain region and in many cases extends somewhat beyond the limits of this physiographic province. It passes more or less gradually into the oak savannah which borders it on the north, west, and south. This area of climax forest also occupies a rough, mountainous region. In fact, it is the most broken area in the state.

The oak-hickory forest dominates throughout the region except for the areas of subclimax pine. Pines usually occupy only the exposed rocky ridges where the soil is poor and thin. Even here there is frequently a considerable admixture of oaks. Certain areas, however, especially in portions of Mc-

Curtain County are clothed by pure stands of pine. Such areas may be regarded as outposts of the subclimax southern evergreen forest. The oak-

Fig. 5. Water oak *(Quercus nigra)* in the climax forest region showing the growth-form where the stand is moderately dense.

hickory forest characterizes the lower protected slopes, and occupies almost all of the comparatively level and more fertile portions of the region. The following species are dominant: *Quercus rubra, Q. schneckii, Q. nigra, Q. velutina, Q. marilandica, Q. stellata, Hicoria ovata, H. laciniosa, H. cordiformis, H. myristicaeformis,* and *H. buckleyi.*

Although often occurring in mictia, the dominants frequently form extensive consociations, *i.e.,* forests in which one species is controlling. Consociations of *Quercus rubra* and *Q. schneckii* are most extensive; the requirements of *Q. marilandica* and *Q. stellata* are so similar that they nearly always occur together; *Q. nigra* forms less extensive consociations, while the hickories are of still less importance.

Deep, fertile, moist soils, especially in northeastern Oklahoma are characterized by *Quercus rubra.* These forests have been extensively cleared and most of the land formerly occupied by them is under cultivation. Small, densely wooded tracts are occasionally found. The trees reach a maximum height of 125 feet and attain diameters sometimes exceeding 4 feet. The largest trees are frequently branched to within 15 feet of the ground and have more or less spreading crowns. The remainder of the stand frequently consists of tall, straight timber, branching only at much greater heights. These trees, which are commonly 90 to 120 years old, have grown up around the spreading parent trees, some of which have reached an age of 200 years or more. In southeastern Oklahoma, similar habitats are occupied by *Quercus schneckii.* These two species are ecological equivalents, except that the former ranges much farther northward. There is some overlapping of their range but where they occur together their habitat preferences seem to differ but little.

The range of *Quercus nigra* is not extensive. It occurs in the extreme eastern and especially the southeastern part of the state. It reaches its best development in fertile level lands where moisture is abundant. Tall, straight trees, two feet in diameter and 70 feet high, are not uncommon (Fig. 5). Much of the land previously occupied by this oak has been cleared for agricultural purposes, but small virgin stands may be found in places not easily accessible. Many woodlots and wooded ravines also still remain in agricultural communities and afford evidence as to the former range of this and other woodland species. Near the border of the woodlands, on fertile hillsides, and in moist ravines this oak is not so tall but the crown spreads more widely. The leaves frequently show remarkable variation. Trees with the typical leafform occur throughout its range but locally the varieties *tridentata* and *hemisphaerica* are frequently abundant. They were usually associated with the typical *Q. nigra* and not infrequently with other oaks and hickories.

Quercus velutina reaches its best development on level uplands and hillsides where the well drained soil is only moderately deep and fertile but of good water content. Fine specimens 50 to 100 feet high with diameters of 15

to 30 inches may be found (Fig. 6). Such trees range in age from 75 to 120 years. Eight to twelve growth-rings per inch of wood are commonly found

FIG. 6. Black oak *(Quercus velutina)* in the central portion of eastern Oklahoma.

under these conditions. This oak also occupies small ravines in the forest or extends along the flood plains of streams into the savannah.

In this climax-forest region, *Quercus stellata* and *Q. marilandica* often reach heights of 50 to more than 75 feet. They have a fairly well developed trunk which is more or less covered with twigs and small branches in open forests but it is smooth and unbranched where the stand is quite close. When the trees reach the level of the general forest canopy the crown branches in the fashion characteristic of the shorter blackjack or post oaks.

The hickories are less abundant than the oaks but they constitute an important element in the forest. They are similar in height to the oaks but the diameters of the trunks are usually smaller. The shagbark hickory *(Hicoria ovata)* is rather commonly found in moist soil. The shellbark hickory *(Hicoria laciniosa)* is found in the northeastern part of the state, while the nutmeg hickory *(H. myristicaeformis)* occurs in the southeast. Both require deep, moist soil. *Hicoria cordiformis,* the bitternut hickory, occurs on less mesic slopes and flats, and *H. buckleyi* alone is able to survive on the driest slopes and ridges.

The deep, fertile, moist soils of hillsides, flats, and valleys in southeastern Oklahoma frequently support well developed, mixed forests of *Quercus schneckii, Q. nigra, Q. phellos, Hicoria ovata,* and *H. myristicaeformis.* The more moist areas are clothed with mixed stands of *H. myristicaeformis* and *Q. nigra* or *Q. phellos,* while the somewhat drier soils are occupied by *Q. schneckii* and *H. ovata.*

In northeastern Oklahoma, *Hicoria ovata, H. laciniosa, H. cordiformis, Quercus rubra,* and *Q. velutina* occupy deep, moist soils. The red oak frequently occurs in pure stands of considerable extent but *Q. velutina* was observed only in mixed stands with other oaks and hickories. *Q. velutina* and *H. cordiformis* are the least mesophytic. *Hicoria alba* is associated with *Q. marilandica* and *Q. stellata* throughout the eastern part of the state on dry hills and uplands. In favorable sites a small percentage of *Q. velutina* is found.

Numerous subdominants occur more or less constantly in mixed stands. The sugar maple *(Acer saccharum)* occurs along steep banks where water content is constantly high and the shade dense. It is so near the edge of its range that it can grow only on the richest soils and is never found in such numbers as to be controlling. *Acer saccharinum* is also abundant in ravines and in rich moist soil. Both species, with rare exceptions, are confined to eastern Oklahoma.

The persimmon *(Diospyros virginiana)* and *Sassafras sassafras* are more important ecologically as shrubs than trees. The former ranges through the savannah and is common in the ravines of the prairie. The latter is less widely distributed and nearly confined to the forested region. Under favor-

able conditions both frequently become large trees, often 2 feet or more in diameter.

Red gum *(Liquidambar styraciflua)* occurs in moist, fertile soil in protected places but thrives best on flood plains (Fig. 7). It frequently attains a

Fig. 7. Young red gums *(Liquidambar styraciflua)* reforesting moist, cut-over areas.

diameter of 2 to 5 feet and a height of 75 to 100 feet. The species is rapidly being cut for lumber. Where the moisture supply is somewhat less abundant, the forest contains a mixture of wild cherry *(Prunus serotina)*, black walnut *(Juglans nigra)*, black locust *(Robinia pseudoacacia)*, black gum *(Nyssa sylvatica)*, and the various species of elm. All of these species drop out near the margin of the climax forest or in the savannah except the elms and walnut which range farther west.

The ironwood *(Ostrya virginiana)* is a small tree which is found on moist, shady slopes and beneath the canopy of rather dense forests. The linden *(Tilia americana)* occurs in deep, moist soil in protected places. In addition to the oaks previously mentioned, the willow oak *(Quercus phellos)*, bur oak *(Quercus macrocarpa)*, and chestnut oak *(Quercus muhlenbergii)* are common. The willow oak is a tree of medium size which develops a rounded conical crown where it is not crowded. It occurs on deep, well drained soils as well as along streams. The chestnut oak is common in valleys and on hillsides near streams where only trees of moderate size occur. The bur oak is common in similar habitats. It is a large, much-branched tree occurring on the uplands and well drained flood plains. The pecan *(Hicoria pecan)* is a tree of frequent occurrence on older flood plains and terraces where it forms tall, dense stands.

The overcup oak *(Quercus lyrata)* and the white oak *(Quercus alba)* are rare, the former being most mesic. They are confined to very moist soils in the extreme eastern part of the state. Least common is the American beech *(Fagus grandifolia)* or one of its varieties which is found only rarely in moist, protected places. The occurrence of certain species both on the flood plains and uplands indicates the prevalence of general mesic conditions in the extreme eastern part of the state.

Numerous small trees, shrubs, and lianas are also common. The shrubs may be divided into three groups. The first is a xeric group, more or less common on dry ridges, rocky slopes, and in similar habitats. The second group is a more mesic one which occurs commonly on hillsides and in ravines. The third is the most mesic of all and occurs only in moist, protected places. In many cases the species are at the extreme limits of their range and frequently very rare.

Shrubs or shrub-like plants of xeric habitats include the Ohio buckeye *(Aesculus glabra)* or one of its varieties. It is found occasionally, attaining a height of only four or five feet. *Ascyrum hypericoides* and *A. stans* are low shrubs found on dry, gravelly slopes and most frequently on southern exposures. The tree huckleberry *(Batodendron arboreum)* is a dwarfed tree or tall shrub occurring on southern slopes in a few localities. The American smoke tree *(Cotinus americanus)* and elastic gum *(Bumelia lanuginosa)* are small trees frequenting dry, rocky slopes. The elastic gum and the two species of *Ascyrum* range westward into the savannah. A chinquapin *(Cas-*

tanea pumila) or a closely related shrubby variety is occasionally found on dry uplands. The small, shrubby trees sometimes reach heights of 15 to 25 feet and the large, clustered involucres with their fruits are often within easy reach. New Jersey tea *(Ceanothus americanus)* and its western form *(C. ovatus)* are low shrubs common to both forest margin and prairie and range far westward. *Grossularia curvata* occurs rarely on high rocky exposures; *Hypericum prolificum, Ilex decidua,* and *I. caroliniana,* the deer berry *(Polycodium stramineum),* a huckleberry *(Vaccinium vacillans),* and the sweet scented sumac *(Schmaltzia crenata),* which is the least common of the sumacs, occur on dry, frequently rocky slopes.

Among the shrubs with an intermediate water requirement and which are of somewhat common occurrence are a number of hawthorns. *Crataegus aspera* and *C. bushii* are found in thickets and open places. *Crataegus marshallii* occurs in ravines and along streams and *C. spathulata* is abundant on hillsides and at the forest margin. The dogwoods *(Cornus amomum* and *C. asperifolia),* the strawberry bush *(Euonymus americanus),* and wahoo *(E. atropurpureus)* are characteristic of thickets and woodlands. Several species of plums *(Prunus americana, P. lanata, P. mexicana,* and *P. munsoniana)* occur in thickets on hillsides and some of them reach the size of small trees in the valleys. The wafer ash *(Ptelea trifoliata)* is a small, bushy tree of infrequent occurrence in scrubby vegetation. Perhaps the most common shrubs are the coralberry and the sumacs. *Symphoricarpos symphoricarpos* is very common in the ecotone between forest and grassland and it is also here that *Rhus glabra* is especially aggressive due to strong development of rhizomes. *Rhus copallina* is the most common shrub of the forest margin. The ill-scented sumac *(Schmaltzia trilobata)* occurs only on sandy or rocky soils and increases in importance westward. *Rhus radicans* and *Rhus toxicodendron* are usually found in the form of low shrubs but the former is occasionally a tall, climbing vine, supported on the trunks of trees by aerial roots. The southern black haw *(Viburnum rufidulum)* is common and widely distributed. The juneberry *(Amelanchier canadensis)* is occasionally found in the transition zone at the forest margin or as a hillside shrub. *Azalea nudiflora* is another species belonging to this group.

The following are shrubs of very mesic habitats: The smooth alder *(Alnus rugosa),* the fringe tree *(Chionanthus virginica),* and the papaw *(Asimina triloba)* occur in damp ravines, on protected slopes, and along streams. The spikenard tree *(Aralia spinosa)* is rare and occurs only in moist habitats. The spice-bush *(Benzoin aestivale)* is rather common in dense woods, where it occurs as an under-shrub, and on protected slopes. The Bermuda mulberry *(Callicarpa americana),* found in moist thickets, and leather wood *(Dirca palustris),* on cool north slopes, are very rare. A wild gooseberry *(Grossularia cynosbati)* occurs only on cool, rocky slopes. The silver-bell tree *(Halesia monticola),* witch hazels *(Hamamelis macrophylla*

and *H. vernalis)*, and *Hydrangea arborescens* are all rare shrubs or small trees found only in moist places. Two species of holly occur; the common Christmas holly *(Ilex opaca)* and *I. decidua* are found in wet places but the latter occurs also on dry slopes. *Magnolia acuminata* is rare, occurring only on shaded slopes and along small mountain streams. As for many other species, this is its extreme western limit. A blackberry *(Rubus frondosus)* is quite frequently found on north slopes and in thickets, and a raspberry *(Rubus occidentalis)* is abundant in openings on fertile flats and is widely scattered among the shrubs especially in the northern part of the state. The Indian cherry *(Rhamnus caroliniana)*, the American bladdernut *(Staphylea trifolia)*, and prickly ash *(Xanthoxylum americanum)*, which are not common and are found only in moist habitats, together with *Cornus florida* complete this group.

A number of lianas not previously mentioned are common among the shrubs and in the woodlands. A grape-like vine *(Ampelopsis cordata)* is commonly found climbing on shrubs and trees. The rattan vine *(Berchemia scandens)* is found in moist woodlands in the extreme east, and the bittersweet *(Celastrus scandens)* is common among shrubs or on small trees in drier places. *Cissus incisa* is a succulent vine found only in rocky soil. The moonseeds *(Epibaterium carolinum* and *Menispermum canadense)* are drupaceous vines frequent in the forests and thickets. The Virginia creeper *(Parthenocissus quinquefolia)* is a common, high climbing liana. Among the species of smilax, *Smilax bona-nox* is of most frequent occurrence; it is adapted to a wide range of conditions and also extends through the central part of the state. *Smilax glauca* occasionally occurs in thickets and open places and *S. hispida*, *S. rotundifolia*, and *S. pseudochina* are found in thickets, valleys, and in many places on north slopes. *Vitis cordifolia* frequently occurs climbing on high trees; *V. rotundifolia* is not a high climber but is found on woody plants of low growth. *Vitis cinerea* also occurs.

SOCIETIES

The herbaceous societies of the deciduous forest are numerous, extensive, and well developed. Only under the densest forest canopy are they reduced to a single, prevernal ground layer and such areas, as a whole, cover only a very limited extent of the region. As in the case of shrubs, many of the herbs, characteristic of the deciduous forest eastward, here reach their western limit of distribution, hence certain societies are found only in the most favorable woodland sites. The societies range from those adapted to marshes and wet lowlands to those of open, dry woods and sterile, rocky outcrops. There is, moreover, an overlapping of the prairie and woodland floras. Species of the former occupy grassy openings in the forest proper and occur in open forests as relicts even after all or nearly all of the grasses have disappeared. Only some of the most frequent and abundant of these species of the prairie are included.

Four seasonal aspects may be distinguished of which the early spring or prevernal and vernal are most marked. This is due to their growth and anthesis largely before the leafing out of the trees, but where the forest is more open aestival and autumnal aspects are also fairly well developed. The distribution of species is closely correlated with the type of woodland and consequently the density of the shade. In the rich, moist soil under the deep shade of the red oak, for example, the plant population is strikingly different from that of the drier, better lighted forests of post and blackjack oak.

Prevernal and vernal societies.—Bloodroot *(Sanguinaria canadensis)*, dutchman's breeches *(Bicuculla cucullaria)*, and wild ginger *(Asarum reflexum)* are among the least widely spread and most mesic species. Somewhat less exacting but also similar in habitat requirements are may-apple *(Podophyllum peltatum)*, and solomon's seal *(Polygonatum commutatum)*, which form conspicuous societies on hillsides and in valleys. *Arisaema triphyllum* and *A. dracontium* are both found in moist, shady places, the latter alone extending westward into central Oklahoma where it is confined to ravines. *Erythronium americanum, Syndesmon thalictroides*, and *Trillium recurvatum* occasionally occur, and the pale blue *Viola missouriensis* and the darker *V. papilionacea* are abundant in dense, moist woods together with the less common yellow *V. eriocarpa* and *V. pubescens*. The annuals, *Valerianella radiata, Caulophyllum thalictroides*, and *Nyctelea nyctelea*, occur along with *Ranunculus micranthus* in deep, moist woods, and the water loving *R. abortivus* is found in wetter soil. In open places where the soil is deep, especially at the margins of forests, *Viola triloba* and *V. palmata* occur. *Ranunculus hispidus* frequents dry, open woods. *Aquilegia canadensis* and *Valerianella longiflora* are less mesic and are found in open, rocky places. *Antennaria campestris* and *A. plantaginifolia*, both species common to prairies, are also frequently found on dry, rather rocky soil in open places especially if the areas are somewhat grass-covered.[1]

Estival societies.—With the passing of the vernal societies numerous estival ones appear although some characteristic species continue to bloom until fall. The tall bellflower *(Campanula americana)*, tick-trefoil *(Meibomia grandiflora)* starry campion *(Silene stellata)*, and *Salvia lyrata* grow in well developed woodlands of moderate shade.

Mesadenia atriplicifolia, Polymnia uvedalia, Monarda fistulosa, and *Lycopus americanus* are robust perennials common in low, moist places. *Teucrium canadense* and *Prunella vulgaris* occur in somewhat drier habitats. Other common species are *Xanthoxalis cymosa, Tovara virginiana, Geum macrophyllum, G. canadense*, and two species of *Bidens*. *Erigeron philadelphicus* is especially conspicuous in moist, open places and *Chamaecrista nictitans* and *C. fasciculata* occur in somewhat drier soils. *Commelina virginica* and *C.*

[1] A complete list of the societies of the deciduous forest is deposited in the botanical libraries of the University of Nebraska and the University of Oklahoma.

crispa begin to bloom in the vernal period and continue until fall. The abundant masses of blue flowers and bright green leaves make them conspicuous among the herbaceous societies. The lopseed *(Phryma leptostachya)*, false spikenard *(Vagnera racemosa)*, together with *Boehmeria cylindrica*, *Pilea pumila*, and *Urtica chamaedryoides* are also among the more important estival plants of the woodlands.

Serotinal societies.—Characteristic autumnal societies are few. The downy lobelia *(Lobelia puberula)* and the many-flowered *Agrimonia parviflora* are late flowering perennials of moist soils. The large leaves of the basal rosettes of *Elephantopus carolinianus* and *E. tomentosus* are conspicuous throughout the summer but their purple flower heads develop only during early autumn. *Aster azureus* and *Boltonia diffusa* occur in rich moist soil near the forest margin where they blossom until frost. Several species of *Eupatorium* are common in moist soils in woods or at their margins. *Eupatorium coelestinum*, with its delicate violet-colored flowers, is found characteristically in rather dense shade where the soil is rich. *E. perfoliatum* and *E. serotinum* frequently make dense growths four to five feet high in moist, open places, while the slender leaved *E. hyssopifolium* is less mesic and sometimes occurs on dry slopes. *Ibidium gracile* is a slender herb found in moderately moist, usually somewhat sandy soil. *Impatiens biflora* is a tall, succulent herb of moist shady places, while *Iresine paniculata* demands more light but also much moisture. The tall, weedy, perennial *Agastache nepetoides* is common in moist woods especially near streams. *Helianthus strumosus* and *H. divaricatus* are robust woodland herbs blossoming from summer until early autumn.

THE SUBCLIMAX PINE *(Pinus echinata)* CONSOCIES

The pine forest community and pines with an admixture of oaks constitute one of the most interesting features of the vegetation of the heavily forested regions of the state. Fine stands of almost pure pine occur in many localities. Such areas frequently consist of tall straight trees 10 to 15 inches in diameter and 100 feet high. The trees are frequently even-aged and of uniform size and in lumbering the area is clean cut. There is usually no reproduction prior to cutting because of the dense shade. Following lumbering operations, however, the growth of young pines immediately begins from seed stored in the forest floor. But suppressed oaks, which are almost universally present as shrubs although often only a foot or two in height, have the advantage of being already on the ground and they rapidly spring into prominence. In the past, the forests have been burned almost every year and fires are still common.

Ecologically the pines represent northern outposts of the coniferous forests of the southeastern United States. Since the settlement of the region, the pines have been utilized and the virgin timber largely destroyed. Pure stands have been cut for lumber and the finer specimens from mixed stands have

also been used to a large extent. Where they were not sufficiently abundant or of a quality desirable for lumber they have been selected in preference to the oaks for poles and rough timbers. Old pine stumps are frequently encountered among the oaks, the latter apparently having never been molested by man. Close observations usually disclose numerous pine seedlings in the vicinity, which, because of their slow growth, are not conspicuous for a period of several years.

The region where pines occur lies entirely within the range of the climax forest but the pines do not dominate except in local areas which are included for the most part in McCurtain County. On the unstable soils of the rugged topography they form a community whose developmental history, in comparison with adjacent ones, points to the fact that it is subclimax and will ultimately be replaced by deciduous forest.

During the early period of lumbering and until 1924, the forests were cut clean. Great tracts were also burned over annually for the purpose of increasing the scant herbage for grazing. In the forested area as a whole there has been a decrease in the amount of pine timber due to its susceptibility to fire injury and particularly to the destruction of the seedlings. The area occupied by oaks has correspondingly increased and many of the cut over tracts have been entirely reforested by them.

Oak-Hickory Savannah

(*Quercus* associes)

This community occupies the region lying west of the climax deciduous forest. It is bounded on the west by a line extending southwestward through Osage county and then only slightly westward to eastern Jefferson county (Fig. 2). It is separated rather sharply from the true prairie on the west by the transition from sandstone soils to the heavier soils originating from clays and shales. The eastern boundary is the climax deciduous forest, but the area is not continuous since a large lobe of the subclimax prairie occurs on the fine textured soils of the northeast. Thus the savannah forms a belt usually 50 or more miles in width extending across the state. Many islands of savannah woodland occur in the true and mixed prairie on sandstone outcrops and tongues extend eastward across sterile ridges and along strips of infertile rocky soil to considerable distances from the margin of the community.

The savannah is characterized by a scrubby growth of oaks usually associated with hickory. Grassland alternating with limited areas of open woodland is characteristic of the northern and southern extremities, while throughout the central part the woodland dominates and grassy areas occur only locally (Fig. 8). Here the forests frequently characterize the landscape for many miles. Thus great variations occur including all degrees of transition from the areas of grassland in the north and south where tree clumps are scattered to the central area where locally woodland predominates (Fig. 9).

Climatically the area should be dominated by grasses but the open, porous soil permits the growth of trees and, in places, turns the balance decidedly in their favor. The Arbuckle Mountains are included in the savannah. The rocky

FIG. 8. Alternes of woodland and grassland in the savannah.

slopes are clothed by forests which are mostly of the blackjack-post oak type. On the steep, most exposed places, cedar *(Juniperus virginiana)* and sumac *(Rhus glabra)* abound. The following are the dominants:—*Quercus marilandica, Q. stellata,* and *Hicoria buckleyi.*

The two oaks are not quite ecological equivalents. The blackjack *(Quercus marilandica)* is a small, often scrubby tree which tolerates dry, sandy or otherwise unfavorable soils (Fig. 10). The blackjack is the more abundant on dry, exposed hillsides or in unfavorable habitats, while the post oak makes up an increasingly greater portion of the timber when habitat conditions are more favorable. Both are characteristic where the association is

well developed. Communities dominated by either species alone are infrequent, that is consocies are not well developed.

Quercus marilandica indicates poor, dry, sterile soils. It is rarely found in rich, moist soils owing to the unsuccessful competition with more tolerant, mesic species. The trees are characteristically small, widely spaced, and accompanied by a shrubby undergrowth. Where shrubs are absent the soil is covered with a more or less open growth of short grasses, especially *Bouteloua gracilis*, the drier places with *Aristida*, if the soil has been disturbed, and with the taller prairie grasses if it is deep and moist. Frequently, however, a dense

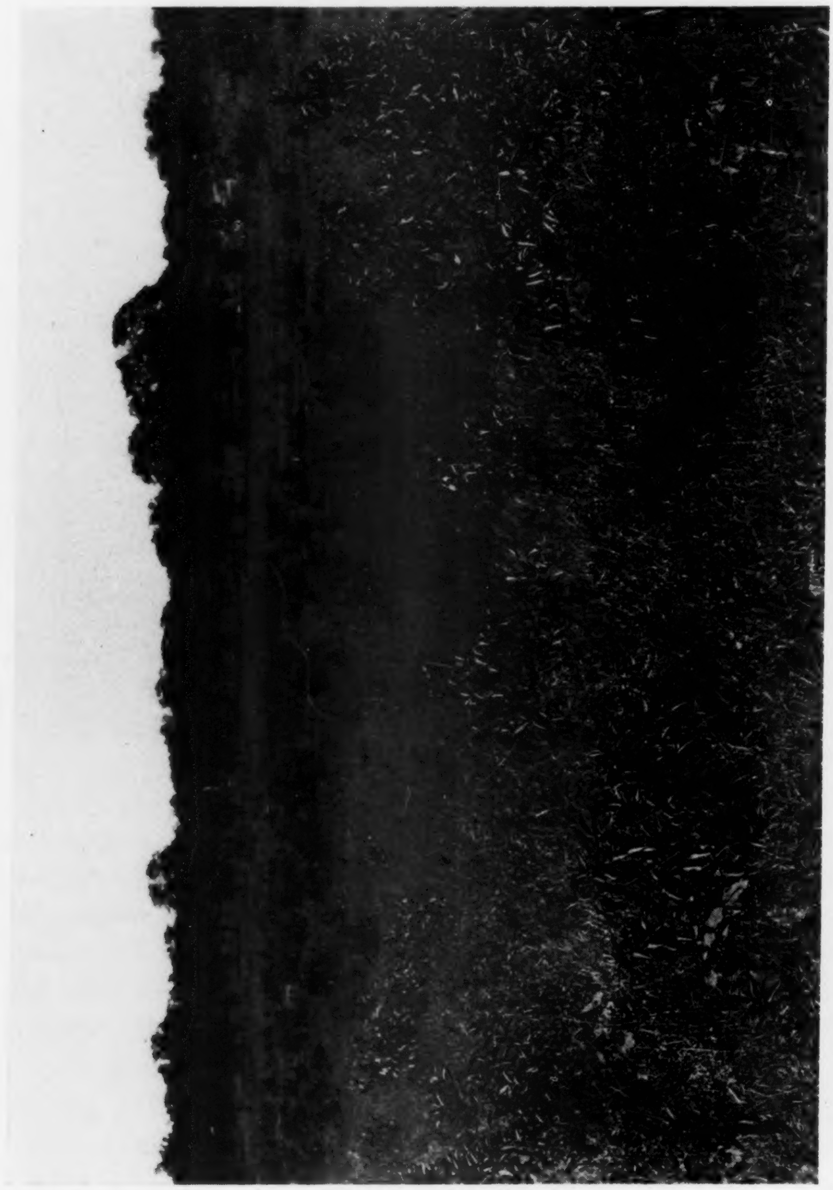

FIG. 9. An open type of savannah woodland in the background and an abandoned field being invaded by persimmons (*Diospyros virginiana*).

layer of shrubby oaks partly or completely covers the soil between the trees and aids in the development of a habitat suitable for the growth of the latter. The growth of the dominant is more vigorous on the lower slopes and in sandy ravines which are too dry and sterile to support the flood-plain type of vegetation. Dense stands occur in such places. Closely spaced trees 15 to 25

FIG. 10. A clump of small blackjack oaks *(Quercus marilandica)* on dry, sandy soil.

feet high with diameters of 3 to 7 inches are of common occurrence in the drier, western part. Under more mesic conditions they sometimes attain a height of 50 feet or more and reach diameters of 15 to 20 inches. This species is not unattractive because of its small size. It has a dark, rather smooth bark and glossy, dark green leaves that are clustered near the tips of the twigs. The spreading, slightly drooping branches, which in open stands form an irregular or dome-shaped top, give a pleasing appearance. It is little used except for fire wood or posts nor is the land it occupies of great agricultural

value. Consequently it is not difficult to find extensive tracts of the undisturbed forest.

Quercus stellata, the post oak, when intermixed with *Q. marilandica,* has much the same habit of growth. The branches are spreading and the peculiarly lobed leaves form stellate clusters on the twigs from which character it received its name (Fig. 11). The bark is much lighter in color than that of the blackjack and has deep fissures between the broken ridges. It reaches a

Fig. 11. Post oak *(Quercus stellata)* showing the typical growth-form in the savannah.

large size on some of the older flood plains but on the upland it is always small or of moderate stature. In mixtures with *Q. marilandica,* the two dominants attain approximately the same size.

The post oak grades almost imperceptibly into a number of shrubby varieties, three of which occur. The common variety found in the savannah is *Quercus stellata margaretta.* The other varieties are western and belong to the chaparral rather than to the savannah.

Hicoria buckleyi is quite commonly scattered among the oaks, especially in the more favorable habitats. It is usually found on soils with slightly more clay and consequently with a somewhat greater water-holding capacity. It occurs more commonly on north or east slopes than on south or west ones. It is usually of about the same size as the oaks among which it grows. It is not associated with the dwarfed oaks of exposed situations but is always intermixed with them where the woodland is well established. Although able to tolerate dry, sandy soils, where it makes only a scrubby growth, more favorable conditions are at once reflected by its greater size.

SOCIETIES

The societies of the savannah fall into two groups, those associated with the wooded areas and those associated with the grassland. The latter are for the most part not here included but are listed under subclimax and true prairie where they also occur. The woodland societies consist of species that are able to grow in relatively sterile, dry soils. The following are characteristic although many also occur on dry, sterile soils of the climax forest.

Prevernal and vernal societies.—Early blooming species are not numerous but the following occur where the woody species afford them some protection: *Scutellaria cordifolia*, *S. parvula*, *Clinopodium glabrum*, *Sanicula canadensis*, *Galium latifolium*, *G. circaezans*, *Xanthoxalis stricta*, *Selenia aurea*, *Pedicularis canadensis*, and *Ranunculus hispidus*. In less sheltered situations the following are found: *Lithospermum carolinense*, *Myosotis virginica*, *Pentstemon hirsutus*, *Erigeron philadelphicus*, *Ionoxalis violacea*, *Ruellia parviflora*, *R. strepens*, and *Tradescantia reflexa*. In dry, exposed places *Cardamine parviflora*, *Plantago virginica*, and *Lesquerella globosa* are occasionally encountered. *Coreopsis grandiflora* and *C. palmata*, inhabitants of moist soil, and the twining *Dolicholus latifolius* of dry sand, all begin to bloom in the late vernal season and the estival period extends well into the summer. The transition from the savannah species of the sandy areas is often quite abrupt as they give way to the more compact soils of the prairie. *Lithospermum carolinense* and *Tradescantia reflexa*, for example, are characteristic of the former and *Lithospermum linearifolium* and *Tradescantia virginiana* of the latter. *Castilleja coccinea* is another common vernal species.

Estival societies.—Under the moderately open canopy of well developed oak scrub such low perennials as *Acalypha gracilens*, *A. virginica*, *Agrimonia mollis*, *A. rostellata*, *Anychia polygonoides*, *Mollugo verticillata*, and *Polgala verticillata* are common on the forest floor. Typical sandy soils of somewhat more open places are characterized by *Meibomia paniculata*, *M. sessilifolia*, *Cracca virginiana*, *Crotalaria rotundifolia*, and *Hypericum punctatum*. Moderately moist and somewhat richer soils support societies of *Sabbatia angularis*, *Buchnera americana*, and *Coreopsis palmata*. The low climbing vines, *Clitoria mariana* and *Galactia volubilis* occur in open places, and the somewhat taller

Strophostyles helvola and *Stylosanthes biflora* are scattered among shrubs and low trees. *Portulaca pilosa*, *Chrysopsis pilosa*, *Gnaphalium purpureum*, and *Croton glandulosus* are typical of dry, exposed openings.

Other common estival species are *Gymnopogon ambiguus*, *Hieracium longipilum*, *Koellia pilosa*, *Parietaria pennsylvanica*, *Polygala ambigua*, and *Tragia ramosa*.

Serotinal societies.—Only a moderate number of late blooming species occurs. *Dasystoma grandiflora* and the decumbent *Lespedeza repens* and *L. procumbens* are found under the typical forest cover. More open places are characterized by *Phaethusa occidentalis*, *Aster patens*, *Solidago tortifolia*, *S. boottii*, *S. ulmifolia*, *Lespedeza stuvei*, and *L. frutescens* which are scattered among the woody species. *Elephantopus carolinianus* is found in moist, shady situations and *Vernonia fasciculata* and *V. baldwinii* in well lighted ravines. *Helenium autumnale* is found only near springs or in similar habitats. More or less barren areas are often occupied by *Diodia teres* and the pinweeds, *Lechea villosa* and *L. tenuifolia*. Characteristic grasses are as follows:—*Andropogon ternarius*, *A. virginicus*, *Aristida gracilis*, *A. wrightii*, *Bromus purgans*, *Carex muhlenbergii*, *Eleusine indica*, *Eragrostis hirsuta*, *E. major*, *E. secundiflora*, *Holcus halepensis*, *Muhlenbergia schreberi*, *M. sobolifera*, *Panicum lanuginosum*, *P. malacophyllum*, *Sitanion elymoides*, *Sporobolus argutus*, *S. neglectus*, and *Uniola latifolia*.

Flood Plain Forests

The vegetation of the flood plains, which extends from the low humid regions of eastern Oklahoma to the high, semiarid western portion, is subject to such varied climatic differences that several types of woodland communities are found.

Communities of Western Oklahoma

In the arid west only trees of the earliest stages in the development of flood-plain forests occur. These pioneers are the black, peach-leaved and sand-bar willows (*Salix nigra*, *S. amygdaloides*, and *S. fluviatilis*) and the western cottonwood (*Populus deltoides*). Even these are found only intermittently along streams where there is a nearly continuous water supply. Neither willows nor cottonwoods reach the stature they attain eastward. Usually the trees are rather widely spaced, a response to the scarcity of water, and the crowns are relatively low and spreading. They are mostly confined to the banks of streams.

White elm (*Ulmus americana*) and box elder (*Acer negundo*) are flood-plain trees which are slightly less xeric than the preceding. They are usually found only near streams or in valleys where the water supply is constant. Where the elms are not protected by deep valleys or stream banks, which break the force of the desiccating winds, the crowns are much flattened as shown in figure 12.

The ill-scented sumac *(Schmaltzia trilobata)* frequently forms isolated thickets which dot the narrow flood plains. Likewise, *Baccharis salicina,* a low shrubby composite common on moist saline or alkaline soils, occupies irregular areas along streams and in the bottoms of dry ravines. These thickets are commonly 2 to 4 feet high and only a few yards in width. They

FIG. 12. White elms *(Ulmus americana)* showing the low spreading crowns characteristic of trees growing along flood plains and ravines in western Oklahoma.

are invaded by white elm, especially throughout the mixed prairie. Hackberry *(Celtis reticulata),* a western black walnut *(Juglans rupestris),* and the wild China-trees *(Sapindus drummondii)* are other xeric species found along stream courses in the west. They constitute a very open fringing forest typical of the narrow flood plains. Even in the most favorable places the hackberry reaches a diameter of only a few inches and a height of 10 to 15 feet, and typically it forms a scraggly shrub-like growth in dry places. The walnuts are small, usually symmetrical trees which frequently form small groves. They seldom exceed 6 to 8 inches in diameter and are 15 to 25 feet in height. They occur typically in ravines or on somewhat protected hillsides. The wild China-tree not only occurs on the flood plains in mixed, open stands with elm, hackberry, and box elder, but is also common in ravines where the small trees often form dense stands.

Deeply eroded hillsides and gullies are likewise dotted with small clumps or with isolated individuals of walnut, mesquite *(Prosopis glandulosa)* and cedars *(Juniperus virginiana).* The mesquite is well adapted to xeric condi-

tions. The small leaves of the somewhat rounded, open crown present a very limited transpiring surface and this is further reduced by the shedding of a part of the leaves during severe drought. The common growth-form is that of a tree although the plants are only 6 to 8 feet high; even the largest are less than a foot in diameter and only 18 to 25 feet tall. The cedars are likewise well adapted to drought. They typically occur on dry, eroded hillsides and on rocky ridges in soil too poor and unstable to support grasses or other herbaceous vegetation. Many of them are old, gnarled and twisted trees with distorted trunks and dead branches which bear evidence of a long struggle against a xeric environment.

A variety of post oak *(Quercus stellata palmeri)* and a smaller oak, which appears to be *Q. vaseyana*, are also sometimes found along stream courses. They are small trees, branched from near the ground and grow in small clumps in the valleys or on the slopes. In the extreme west they are usually only 2 to 3 inches in diameter and 10 to 15 feet high.

Communities of Central Oklahoma

The flood plain vegetation increases both in number of species and luxuriance of growth as the habitat becomes less arid toward the central part of the state. Cottonwoods and elms, for example, become closely spaced and tall, unbranched trees replace the low spreading forms except in the most exposed places. As the forests become better developed and more extensive they also increase in complexity of structure. The few xeric species of the west are for the most part replaced by a larger number of mesic ones. Mesquite, which is near the limit of its range even in western Oklahoma, disappears. *Juglans rupestris* is replaced by its mesic relative *Juglans nigra*. *Celtis reticulata* gives way to *C. occidentalis* and *C. mississippiensis*. The shrubby, western varieties of oaks and *Baccharis salicina* disappear and *Schmaltzia trilobata* becomes relatively unimportant. The wild China-tree becomes much less important and *Rhus glabra*, *R. copallina*, *Diospyros virginiana*, and *Symphoricarpos symphoricarpos* become the most important shrubs in the ravines.

The sere on the flood plain is initiated with seedlings of *Salix fluviatilis*, *S. nigra*, *S. amygdaloides*, or *Populus deltoides* on the alluvial deposits which are frequently of sand. With the development of the woodland, the intolerant tree pioneers are at first partially and finally almost completely replaced by more tolerant species. The most important are *Ulmus americana*, *Fraxinus americana*, *Juglans nigra*, *Hicoria pecan*, and *Diospyros virginiana*. Of less importance, although often abundant, are *Ulmus alata*, *Celtis occidentalis*, and *Cercis canadensis*. A third stage in development is represented by a consocies of oaks. It consists of an intermixture of *Quercus macrocarpa*, *Q. michauxii*, *Q. schneckii*, and *Q. velutina*.

COMMUNITIES OF EASTERN OKLAHOMA

Many factors combine to produce mesic conditions in eastern Oklahoma. Chief among these are the low altitude (about 400 feet), a rainfall of about

FIG. 13. Cypress *(Taxodium distichum)* on the banks of a sluggish stream in southeastern Oklahoma.

40 inches, and relatively high humidity. The rich, alluvial flood plains of the main rivers are well developed and even the smaller streams continuously flow from the forested hills and mountains. Consequently, the forest is rich in species of trees, shrubs, vines, and herbs.

The most hydric of the trees is the bald Cypress *(Taxodium distichum).* It is a tall, graceful tree with a symmetrical trunk the base of which is sometimes moderately buttressed. They are frequently 2 to 4 feet in diameter and 100 feet high (Fig. 13). Streams and ponds of the extreme southeast are frequently characterized by a fringe of cypress.

The sweet or red gum *(Liquidambar styraciflua)* is another important flood-plain species of the southeast. It is especially common on swampy or rich, bottom-land soils and is frequently the most important species in reforesting cut-over areas. It also invades abandoned fields and thrives even on moderately dry soil.

The sycamore *(Platanus occidentalis)* is one of the most rapidly growing trees as well as one of the largest of the flood plain. It reaches its greatest size in the northeastern part of the state where it is common. Here trees ranging from about 100 feet in height and 2.5 to 3 feet in diameter were found to be approximately 90 years old (Fig. 14).

The red birch *(Betula nigra)* is common but rather scattered in occurrence. It is frequent in wet habitats along the banks of streams in the climax forest area and may be found even in the savannah where it also grows along streams.

Black gum *(Nyssa sylvatica)* is usually confined to the flood plains but also occurs on hillsides in deep fertile soil. It frequently becomes a tall, rather straight tree 2 feet in diameter and 75 feet high. It nearly always occurs in mixture with other trees on the flood plain.

Various other trees and shrubs which are not found westward occur in these flood-plain forests. Among these are *Sassafras sassafras, Toxylon pomiferum, Morus rubra, Alnus rugosa, Aralia spinosa, Ilex opaca, Rhamnus caroliniana, Xanthoxylum clava-herculis,* and *Cynoxylon floridum.* The more mesic lianas are represented by *Epibaterium, Passiflora, Berchemia,* etc. Many dominants of the central Oklahoma flood plains such as elms, hackberries, walnut, black and honey locust, etc., here make a wonderful development, indeed, finer specimens would be difficult to find. As a rule these forests are mixed, and further study is needed to determine their structure in detail. On the older flood plains they give way to the climax forests of oak and hickory already described.

The general decrease in development of forest trees both of the flood plain and uplands from east to west is shown in Table VI. The decrease in size and the rate of growth, however, is no more marked than the change from the tall, upright form eastward contrasted to the low branching form in the west. Of the 80 woody species of eastern Oklahoma, only 43 occur in the savannah and

flood plains of the central part and this is reduced to 9 in the west. This does not include the 7 woody species found only in the drier parts of the state.

FIG. 14. Sycamore *(Platanus occidentalis)* and red oak *(Quercus rubra)* showing the tall, unbranched form common in the east.

Table VI. *Relative stature and rate of growth of various species in western, central, and eastern Oklahoma.*

Species	Place	Height in feet	Diameter in inches	Height to branches in feet	Years for one inch growth in diameter
Populus deltoides	W	20– 50	6–30	10–20	4– 8
	C	50– 75	20–40	20–40	3– 4
Ulmus americana	W	10– 30	6–10	8–10	6–12
	C	25– 50	10–20	10–25	4– 8
	E	50– 75	20–36	30–40	3– 5
Fraxinus pennsylvanica	W	10– 15	6– 8	6– 8	8–12
	C	20– 30	8–16	10–15	4– 6
	E	40– 60	12–20	25–45	3– 4
Quercus macrocarpa	C	30– 50	20–40	10–25	6– 8
	E	50– 75	30–50	.....	5– 6
Quercus stellata	C	15– 30	8–12	5–15	10–18
	E	40– 70	10–20	20–40	5– 6
Quercus marilandica	C	15– 25	8–12	6 –15	10–18
	E	40– 70	8–18	20–40	5– 8
Quercus rubra	C	50– 75	10–18	25–40	8–10
	E	75–100	20–40	40–60	4– 5

The Chaparral

(*Rhus-Quercus* Associes)

The chaparral is a shrub community which is found at the margin of the deciduous forest and forms an ecotone between it and the grassland. It is of low, woody growth and occurs in habitats that are too dry for the development of trees. It consists of fringing belts of shrubs and tongues of shrubby growth which extend into the grassland along the streams and ravines.

The chaparral is best developed and richest in species where it occurs at the margins of the deciduous forest but is most extensive westward in the general savannah region, although the component species are fewer. As it extends up the valleys across the grassland, it becomes still further modified both in appearance and composition, for here the growth of shrubs is increasingly difficult owing to increased aridity accompanied by drying winds.

The following list of woody species includes a number of trees (such as *Celtis reticulata, Fraxinus pennsylvanica,* and *Quercus marilandica*) which, under these xeric conditions, form a scrubby growth often only 5 to 8 feet high:— *Artemisia filifolia, Ceanothus ovatus, Celtis reticulata, Cephalanthus occidentalis, Cornus amomum, C. asperifolia, Diospyros virginiana, Fraxinus pennsylvanica, Prunus americana, P. angustifolia, Quercus marilandica, Q. mohriana, Q. prinoides, Q. stellata margaretta, Q. stellata palmeri, Q. stellata*

rufescens, Q. vaseyana, Rhus copallina, R. glabra, Sambucus canadensis, Schmaltzia trilobata, Symphoricarpos symphoricarpos, and *Yucca glauca.*

The chaparral is represented in the central part of western Oklahoma by communities of "shin oak." Here *Quercus mohriana, Q. stellata palmeri, Q.*

FIG. 15. Circular zones due to radial migration of shin oak *(Quercus mohriana)* in central Oklahoma.

s. rufescens, and *Q. vaseyana* occupy sandy areas and are especially abundant in overgrazed pastures and abandoned fields. Great, circular zones indicate that the oaks have rapidly spread throughout a period of many years (Fig. 15). The oldest, central part, often 25 to 50 or more meters in diameter, consists of small trees 10 to 15 feet high and very closely spaced. Frequently, five to ten such scrubby trees, some of which are 2.5 inches in diameter, occur per square meter. The margins of the areas consist of low shrubby oaks which are, perhaps, only 2 feet tall, but they frequently bear an abundance of large acorns. Here 50 to 100 slender sprouts occur in an area of a square meter while a few feet from the margin they have been reduced by competition to 20 or 30 branching, slightly taller stalks per unit area. Numerous grasses and herbaceous plants, which are common on sandy soil, are found among the oaks near the margin. By the time the latter are 3 feet high, however, the shade is so dense that practically all but the oaks have disappeared.

Westward from the savannah, extensive areas of sandy soil are occupied by *Artemisia filifolia,* development of the sand sage being encouraged by overgrazing. Pastures were studied which were completely covered with

sage so dense that scarcely a spear of grass or a leaf of herbaceous vegetation could be found among the shrubs, although similar soils in adjacent areas had only a moderate amount of sage.

Another important shrub of the west is the stinking sumac *(Schmaltzia trilobata)* which forms thickets, frequently more or less circular and only 2 or 3 feet high, which are so dense as to exclude almost all other species. An elm, boxelder, or other tree occasionally may be found in these thickets but herbs are practically kept out. The spreading, lower stems come in contact with the soil and soon become more or less completely covered with earth and humus and firmly rooted so that the erect branches are attached to a dense interlacing network of buried stems. Other less important chaparral species of the west are *Celtis reticulata, Cornus asperifolia,* and *Prunus angustifolia.* Many others occur eastward, especially where the chaparral is in contact with the flood-plain forest.

The composition of the chaparral varies with the communities with which it is in contact. The most common types are those of the ecotone separating the oak-hickory forest from the true prairie; the ecotone between woodlands of ravines and the true prairie; and that between the flood-plain forest and the subclimax prairie.

The transition from oak-hickory forest to true prairie is most commonly made by various mixtures of *Symphoricarpos symphoricarpos, Rhus copallina, R. glabra, Quercus stellata margaretta, Q. marilandica,* and *Q. prinoides.* Frequently *Symphoricarpos* is absent and also, not uncommonly, the sumacs. The ecotone then consists of a low growth of *Q. prinoides* intermingled with the grasses at the margin as is shown in Fig. 16. Nearer the forest proper, *Q. stellata margaretta* and dwarfed specimens of *Q. marilandica* form low clumps which give way to the typical tree-forms. All of the oaks sprout vigorously and dense stands of more or less alternating areas quickly occupy cleared places or advance slowly into the grassland where the latter is not stabilized. Of the two sumacs, *Rhus copallina* appears to be slightly the more mesic since it becomes more abundant eastward. Both are also common in the ecotone. These pioneer into the grassland and their advance by rhizomes is fairly rapid wherever there is a surplus of available soil moisture. *Symphoricarpos* is more tolerant of shade than the sumacs and is frequently associated either with them or with the oaks as an understory.

Ravines in the prairie frequently support chaparral communities in which the oaks are absent. *Symphoricarpos symphoricarpos, Rhus glabra, R. copallina,* and, occasionally, *Sambucus canadensis, Prunus angustifolia,* and *Schmaltzia trilobata* in sandy soil, are succeeded by *Prunus americana, Ulmus americana, Acer negundo, Fraxinus viridis, Cercis canadensis,* and *Quercus macrocarpa.* These with an admixture of other species form a transition to the flood-plain forest.

The chaparral fringe between the flood-plain forest and the subclimax prairie consists of the following species: *Cornus asperifolia, Cornus amomum, Rhus glabra, R. copallina, Cephalanthus occidentalis,* and *Diospyros virginiana.* All are true shrubs except the last which frequently becomes a small tree 6 to 8 inches in diameter and 25 feet or more high. It forms dense thickets in ravines as well as along flood plains and frequently occurs in pure stands. The shrubby growth is replaced by the development of low groves as

FIG. 16. *Quercus prinoides* showing the typical growth form. Acorns were abundant in this community.

the suppressed species die and the dominants make a vigorous growth. Thus, once in possession of the habitat, it is not replaced by other species as quickly as are the other shrubs. Ultimately, however, it may be succeeded by the taller trees of the forest.

The ecological requirements of the chaparral species are intermediate between those of the prairie and forest. Shrubs become established in localities where the water content is favorable. Their reactions result in a more mesic habitat from which they spread, sometimes by seeds but more commonly by vegetative propagation, into the drier surrounding areas. Eventually, if fires, grazing animals, and man permit, an equilibrium is reached. The shrubs are unable to advance farther into the grassland because of the decreasing water content. The grasses are able successfully to compete with the shrubs by reducing the water content below that required for the development of the shrubby seedlings or off-shoots. When such a degree of stabilization is at-

tained, the shrub associes become relatively fixed as to location and continue without much change for long periods of time. Minor fluctuations due to a series of wet or dry years are noticeable at the margins but the areas as a whole are quite constant. Many shrub communities, however, showed marked evidence of developmental activities. These are especially common in moist ravines and on flood plains where reproduction and size of individuals make it evident that succession has been rather rapid at least for the last twenty or thirty years.

The Grassland Formation

(*Andropogon* associes)

The *Andropogon* associes constitutes the subclimax prairie of eastern Oklahoma and is also represented extensively in the postclimax prairie of the sandy soils which occur along river courses throughout the true and mixed prairies and even in the short-grass plains.

The subclimax prairie lies west of the northern area of the deciduous forest and extends from Washington to Ottawa Counties along the northern border and southward a short distance beyond the South Canadian River (Fig. 2). Only isolated tracts occur further southward and according to Tharp (1926) it is not represented in Texas. This tall-grass prairie represents the southern extension of a vast grassland area which borders the forests and ranges northward to Minnesota (Clements, 1920). It occupies an area where the vegetation, because of unfavorable edaphic conditions, recurrent fires, or other reasons has not developed to the point where it is in harmony with the climate, which is essentially similar to that of the deciduous forest. Shrubs have frequently been observed invading this grassland especially in the northeast which is in the region of highest rainfall and lowest evaporation.

The postclimax prairie is an edaphic associes which occurs as numerous large belts and islands in the climax grassland area. It occupies the Tertiary deposits of sand which form extensive areas along the streams and large isolated tracts in the Redbeds and Gypsum Hills. The associes is characterized by tall, coarse grasses, most of which are also dominants of the subclimax prairie, a fact that indicates that the vegetation has not yet developed to a stage where it is in equilibrium with the prairie-plains climate. As is shown in Fig. 2, the consocies occupies sandy areas in the true prairie, in the mixed prairie, and to a more limited extent even in the short-grass plains. Notwithstanding that the habitat is subject to the hot winds and decreasing humidity which characterize the several climax grassland associations, except for a decrease in the luxuriance of the vegetative growth westward, this postclimax grassland is quite similar throughout. In the utilization of these grasslands the sandy soils and high winds make it imperative that the ranges be judiciously grazed and that most of the soil remains unbroken, otherwise excessive wind erosion follows the loosening of the soil either by trampling

herds or cultivation. The dominants of the associes are: *Andropogon furcatus, A. chrysocomus, A. hallii, A. nutans, A. scoparius, A. saccharoides, Bouteloua racemosa, Elymus canadensis, Panicum virgatum,* and *Spartina michauxiana.*

The associes is characterized by a luxuriant growth of tall grasses. It is in this forest climate that the grasses make their maximum development. The tall grasses of the subclimax prairie moreover, characterize this particular stage in the development of vegetation and, with few exceptions, are not dominants elsewhere.

The most typical expression of the subclimax prairie of eastern Oklahoma is found in alternations and mictia of *Andropogon furcatus, A. nutans, A scoparius,* and *Bouteloua racemosa.* The big bluestem *(Andropogon furcatus)* is found in slight depressions or on more moist slopes where it is frequently associated with *Andropogon nutans.* Its relation to the true prairie is shown by the fact that slightly drier slopes and areas which are more exposed or better drained are occupied by *Andropogon scoparius* which is usually accompanied by *Bouteloua racemosa.* Where the soil is still more moist than that occupied by the big bluestem, *Panicum virgatum* is usually dominant. In ravines or depressions or areas where the soils have a slightly coarse texture, *Panicum* dominates or alternates with the big bluestem. The quadrats in Fig. 17 show the typical relations of the dominants. *Elymus*

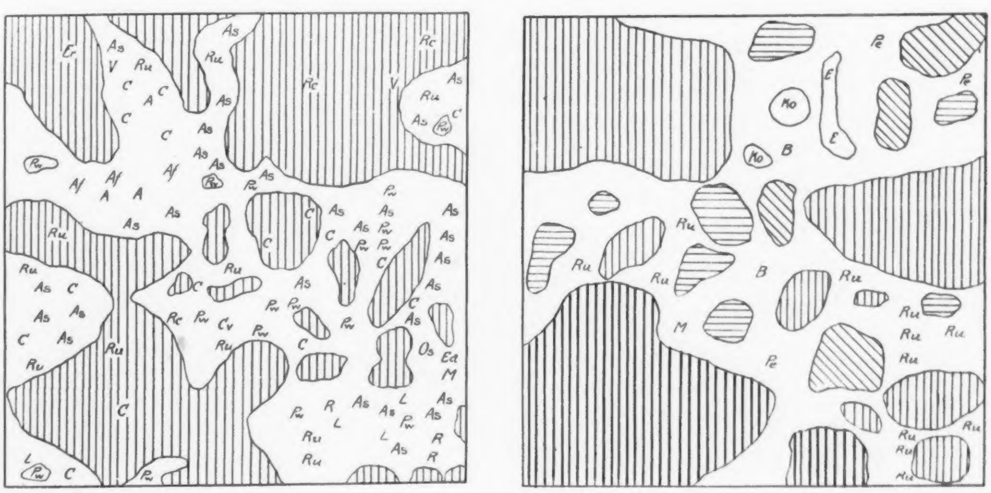

FIG. 17. Typical quadrats in subclimax prairie. Af or vertical hatch, *Andropogon furcatus;* As or horizontal hatch, *A. scoparius;* P or left hatch, *Panicum virgatum;* B, *Bouteloua racemosa;* Ko, *Koeleria cristata;* Pw, *Panicum wilcoxianum;* other symbols indicate forbs.

has much the same requirements as *Panicum* and is found especially where the soil has been disturbed. Areas with a very high water content are characterized by sloughgrass, *Spartina michauxiana.* Sloughgrass occurs only where the soil is saturated at intervals.

Andropogon furcatus is the most characteristic dominant in the eastern half of the state but is also important in the postclimax prairie. It is conspicuous because of its size, abundance, and general distribution. It requires a deep, moist soil for its best development where it commonly reaches a height of 6 to 8 feet. The average yield of this grass per square meter in a dense stand where the plants were 6 feet high after the flowering stalks had developed, was 1478 grams. In fact, its great vegetative growth makes it one of the most important grasses for grazing and for hay. To obtain the best quality of hay, however, it should be cut before the coarse, woody flower stalks develop.

The sand tolerant *Andropogon chrysocomus* is the characteristic dominant in the edaphic, western extensions of the andropogon associes but it is ecologically unimportant elsewhere (Fig. 18). Usually it is less rank in its

FIG. 18. *Andropogon chrysochomus*, a dominant in the postclimax portion of the *Andropogon* associes.

vegetative growth than *A. furcatus* and in the flowering stage the stalks as well as the conspicuous bristles of the inflorescence are more golden in color. This feature accounts for its common name, yellow-haired beard grass. Earlier in the season, while in a vegetative condition, it is frequently difficult to distinguish it from *A. furcatus*, but it is usually more glaucous and ex-

hibits a growth which is slightly less luxuriant. It commonly grows 4 feet high and in a pure dense stand the yield may be equal to that of *A. furcatus* of a similar height and density. This dominant is of great importance as a pasture and hay-meadow grass. The sandy soils in which it grows have not been extensively broken for farming.

Andropogon nutans is listed among the consocies due to the fact that it attains this rank in the subclimax prairie as a whole (Clements, 1920). In Oklahoma it occurs throughout the associes and although a constant associate of *A. furcatus* and *A. chrysocomus* it rarely if ever attains consocial rank. Usually it occupies only a small percentage of the total area.

Andropogon scoparius is the dominant grass in the drier, more exposed portions of the subclimax prairie. It is especially adapted to thrive in such localities due to its adjustment to soils having a relatively low water content, in this respect making the least demands of any of the dominants. It ranges throughout the associes and is common both in the east and west. Its finely divided but extensive root system and relatively smaller development of the parts above ground fit it as a dominant of the true prairie also; hence, its wide distribution. It is important in pastures and hay meadows where it ordinarily reaches a height of 20 to 30 inches. *Bouteloua racemosa* is usually associated with *Andropogon scoparius* and *A. saccharoides* but is occasionally a dominant of rather local occurrence.

Elymus canadensis, together with *E. virginicus* and *E. striatus*, is characteristic of the *Andropogon* associes. Although important components of the tall-grass prairie, even *E. canadensis* is not an extensive dominant. These species develop a luxuriant foliage earlier in the spring than most of the other grasses. The period of flowering and seed development begins by midsummer when most of the other grasses are still in the vegetative state. Flower stalks of *E. canadensis* and *E. virginicus* are commonly 30 to 40 inches high but those of *E. striatus* are usually only about 18 inches tall. Before the plants mature, their foliage is excellent for forage. Cattle eat these species in spring when the leaves are tender but as they become coarser preference is given to the andropogons.

Panicum virgatum in its vegetative condition is a coarse dark green grass in comparison with the andropogons. Later in the season the stems, topped by bushy panicles, sharply contrast with the bronze, green, and gold of the reed-like bluestems. It is abundantly found where the water content is high as in depressions or ravines and especially on porous, sandy soils where it forms consocies.

Spartina michauxiana is common in wet habitats where it may dominate limited areas. It indicates the transition from the reed-swamp stage to grassland. It is not a dominant of consocial rank in Oklahoma although it attains this importance northward (Clements, 1920). It is the most hydric of the tall grasses and frequently grows in soils which are periodically submerged

in shallow water, although during drought the habitat frequently becomes quite xeric. *Spartina* shows adaptations to these varying conditions in the abundant aerenchyma in the cortex of the roots which aids in aeration when the soil is saturated. The deeply penetrating roots are efficient absorbing organs during periods when the upper layer of soil is dry (Weaver, 1920). The leaves are heavily cutinized and hence protected against evaporation in the dry, hot summer. It forms dense, sodded areas which increase in size as a result of propagation by strong rhizomes. Although sometimes cut for hay, its chief rôle is that of soil accumulation and formation.

Tripsacum dactyloides is a coarse, harsh grass common to wet habitats. It occurs as far west as Woods County.

Andropogon glomeratus is not abundant and does not form pure stands but usually grows in small, scattered bunches. Frequently a few stalks form small clumps among the more abundant grasses and sedges of very wet habitats. During the period of flowering the tall, reed-like flower stalks frequently extend two or three feet above the other vegetation. As the compact head-like inflorescence becomes heavier, the slender stalks gracefully bend until the tips nearly touch the ground. It is of local occurrence and of little economic importance.

Many grasses, sedges, and rushes of secondary or minor importance occur in this associes. They are especially abundant in places unsuitable for the formation of sod by the big bluestem or other sod forming dominants. Two or more species of each of the following genera occur: *Agrostis, Carex, Juncus, Chaetochloa, Eragrostis, Cyperus, Panicum, Paspalum,* and *Phalaris.* Other species are *Fuirena hispida, Rynchospora cymosa,* and *Scleria oligantha. Distichlis spicata* occasionally occurs on alkali flats.

Socies of the Subclimax Prairie

The subclimax prairie is especially rich in species forming socies (Fig. 19). Practically all of the species forming societies in true prairie are present and as a result of the favorable moisture relations their growth is usually more luxuriant than in the true prairie. The rich prairie flora is supplemented somewhat by the invasion of species from woodland and forest margin whose presence is one of the indicators of subclimax conditions.

Prevernal and vernal socies.—The moist, prevernal season of the subclimax prairie is especially characterized by the grass-like *Sisyrinchium albidum* and *Hypoxis hirsuta,* light-blue wild hyacinth *(Quamasia hyacinthina),* narrow-leaved collinsia *(Collinsia violacea),* dwarf dandelion *(Cynthia dandelion),* a violet *(Viola* sp.), and prairie crowfoot *(Ranunculus ovalis).*

Although some of these socies continue into the vernal aspect, the landscape is for the most part characterized by new and more conspicuous ones. *Baptisia leucantha* is especially abundant, holding its bushy crown and white-flowered racemes well above the level of the other herbs. It frequently be-

comes three to four feet tall. *Baptisia australis* is also a tall legume; it is characterized by conspicuous blue flowers. Both occur along with *Allium canadense, Tradescantia reflexa, Delphinium virescens, Hartmannia speciosa, Polygala viridescens,* and *Vicia americana.* A little later *Coreopsis lanceolata, Daucus pusillus, Ptilimnium nuttallii, Eryngium aquaticum,* and *Glycyrrhiza* become prominent among the tall grasses. *Potentilla canadensis, Amsonia amsonia, Eustoma russellianum, Vagnera stellata,* and *Lobelia spicata* are common in moist ravines, while on drier or more exposed slopes *Kneiffia linifolia, Cathartolinum medium,* and *Trifolium carolinianum* are found. Eroding, rocky banks and ridges frequently support magnificent clumps of *Megapterium missouriense. Sitilias caroliniana, Bellis integrifolia, Phacelia*

FIG. 19. *Echinacea paradoxa, Petalostemon candidus,* and *Liatris scariosa* in the subclimax prairie.

dubia, and *Parosela aurea* also occur. Where the vernal aspect is fully developed, the blossoming of *Psoralea tenuiflora* and *P. esculenta* indicates the approach of the estival period during which the psoraleas reach their maximum development. Other species are *Alsinopsis nuttallii, Fragaria virginiana, Phlox pilosa, Psoralea simplex, Rubus trivialis,* and *Specularia perfoliata.*

Estival socies.—The mesic tall-grass prairies are characterized during the summer by *Petalostemon multiflorus, P. candidus, P. purpureus, Meibomia illinoensis, Mesadenia tuberosa, Rudbeckia grandiflora, Ptilimnium capillaceum,* and *Asclepias sullivantii.* Tall, rank growths of *Cicuta maculata, Dracopis amplexicaulis, Sesban macrocarpa, Rudbeckia maxima,* and *R. triloba* are found in ravines and other moist places. *Oenothera biennis,*

Gaura biennis, and *Lactuca ludoviciana* also occur where the water content is high. *Echinacea paradoxa* is an early estival species occurring on barren, eroding slopes. *Acuan illinoensis*, *Commelina virginica*, *Erigeron ramosus*, *Pentstemon gracilis*, *Sabbatia angularis*, *Thelesperma trifidum*, and *Zizia aurea* also belong to this group.

Serotinal socies.—The appearance of various species of *Solidago*, *Aster*, *Silphium*, *Vernonia*, and numerous other late flowering species, which are for the most part composites, indicates the approach of the serotinal period. The composites especially characterize the grasslands in autumn, at least as far west as the short-grass plains where societies are much less abundant. Most of the late-blooming true prairie species occur in the subclimax prairie but the blazing stars *(Lacinaria)* are especially conspicuous. *Lacinaria scariosa* appears to be confined to the subclimax prairie where *L. pycnostachya* and *L. squarrosa* are also most abundant but these also occur westward. *Vernonia crinita*, *V. fasciculata*, *Eupatorium hyssopifolium*, *E. serotinum*, and *E. perfoliatum* are of frequent occurrence in moist depressions. Other serotinal species are *Solidago ulmifolia*, *S. rigida*, and *S. radula*, which disappear relatively early in the fall, but *Aster salicifolius* and *A. paludosus* frequently persist until killed by frost.

Socies of the Postclimax Prairie

The westward extension of the *Andropogon* associes, *i.e.*, the postclimax areas, has numerous peculiarities which make it distinct from the subclimax andropogon prairie. Certain plants characteristic of sandy soils are found among the socies. The flora is strongly influenced, moreover, by the floras of the bordering grasslands of true and mixed prairie and short-grass plains. Nearly all of the grassland herbs may be found.

The most striking species forming socies is the beautiful white-rayed *Aphanostephus skirrobasis* which, when at its maximum, frequently gives an almost snowy whiteness to the prairie. In pastures, especially, it is frequently associated with the tall, white-flowered prickly poppy *(Argemone intermedia)* and the somewhat lower, bushy *Cnidoscolus stimulosus*. The latter is also a beautiful, white-flowered, sand-loving plant but extremely disagreeable because of its stinging spines. *Cnidoscolus texanus* less commonly occurs in the southern portion; it is an ecological equivalent of *C. stimulosus*. The dayflower *(Commelina virginica)* forms attractive mats, has pretty blue blossoms, and like *Cracca virginiana* is especially common in the eastern portion of the postclimax prairie. Species of *Eriogonum*, *Froelichia*, and *Heliotropium* form outstanding socies in this community. *Oenothera grandiflora* is common in the moist ravines even far into the western portion of the state. *Stillingia sylvatica* is plentiful on grassy hillsides. Species of *Strophostyles* frequently occur on active dunes along the streams. The following are also characteristic species: *Achillea lanulosa*, *Agalinis*

aspera, A. besseyana, Asclepias arenaria, A. tuberosa, Berlandiera texana, Buchnera americana, Chamaesyce glyptosperma, Corispermum hyssopifolium, Croton glandulosus, Daucus carota, Diodia teres, Gilia longiflora, Hibiscus trionum, Ibidium gracile, Iva ciliata, Othake callosum, Otophylla densiflora, Meibomia sessilifolia, Parosela nana, P. lanata, Pentstemon pallidus, Petalostemon candidus, P. purpureus, P. villosum, Physalis pubescens, Plantago purshii, Polygala alba, Ptilimnium capillaceum, P. nuttallii, Reverchonia arenaria, and *Salsola pestifer.*

Characteristic grasses and grass-like species include the following: *Aristida curtissii, A. fasciculata, Calamovilfa gigantea, C. longifolia, Carex bicknellii, Cenchrus carolinianus, Cyperus houghtoni, C. schweinitzii, Paspalum laeve, P. stramineum, Redfieldia flexuosa,* and *Sporobolus cryptandrus.*

SUCCESSION IN THE POSTCLIMAX PRAIRIE

The sandy prairies are especially interesting from the standpoint of succession. The greater portion of the substratum is, of course, in a fairly stable condition, but along the streams small dunes are still in the process of formation and a few rather large active dunes occur (Fig. 20). Probably the

FIG. 20. Shifting sand dunes are found in only a few localities in western Oklahoma. Those near Waynoka are most extensive.

origin of all the sand dunes was by a process somewhat similar to that which is in progress today, although perhaps on a much larger scale. The streams flowing over deposits of sand redistribute this material in the channel but in

time of high water the flood plains also receive extensive deposits. After the flood the water recedes into a narrow channel leaving the wide expanses of sand to dry and be blown into dunes by the almost constant winds. Aided by the growth of ruderal vegetation and willows, which retard the wind-blown sand, the dry portion of the channel often becomes filled with billowy dunes 6 feet high and hundreds of yards long. The winds, however, do not confine their action to the river bed. Sweeping down the channel for miles they carry along a constant stream of sand which wears away the banks of the river and drifts the materials into fresh dunes on the flood plain. In this way dunes 10 to 20 feet high and several hundred feet long are built in the course of 3 or 4 years. Frequently they are destroyed by high water but some of them eventually become covered with vegetation. Thus, bare areas are produced which afford places for studying successional development and they permit the reconstruction of a complete sere.

In addition to the coarser particles dropped by the wind in the building of dunes, great quantities of fine sand and dust are carried many miles during storms. Where some obstacle breaks the force of the wind, a layer of dust, sometimes a centimeter thick, is deposited on the surface of the soil at a distance of three miles from the river in a single afternoon. Deposits of such material have a marked influence on the vegetation occupying the sandy belts of soil bordering the rivers.

Andropogon chrysocomus is capable of emerging from small sand drifts whereupon it forms large, dense clumps which spread radially into the unstable soil. It can compete successfully with any of the ruderal species which are always more or less abundant in such areas. *Panicum virgatum* behaves similarly in rather low areas. The shoots emerge from the shallower portions of the drift and the roots and rhizomes effectively bind the soil. On high dunes where the sand is dry as well as in lower places, *Calamovilfa gigantea* is frequently an important sand-binding plant (Fig. 21). Numerous characteristic socies also occur. *Reverchonia arenaria* is frequently abundant in the earliest stages of revegetation. *Chamaesyce glyptosperma* and other species of this genus also frequently occur in similar places. *Othake callosum, Strophostyles helvola, Parosela nana,* and *Heliotropium convolvulaceum* are frequent in loose sand if it is not deep. Numerous ruderal species such as sunflowers, ragweeds, prickly poppy, Russian thistles, cockleburs, and *Iva ciliata* are also common.

Various woody plants frequently occupy the dunes for long periods of time; numerous thickets of various species of plums are examples. They are not uncommonly associated with *Smilax* especially where the thickets are rather open, and poison ivy and ill-scented sumac also occur. Cottonwoods and willows are often found in depressions while blackjack and post oak not infrequently become established and persist indefinitely, especially in the eastern portion.

Species whose roots penetrate deeply are able to ecize because of the fact that the layer of sterile sand frequently covers a more fertile substratum. With an increase in organic matter the fertility and water-holding capacity of the soil greatly increase and the dominant grasses more and more completely gain control. Reproduction of woody plants is difficult in this windswept region, and upon the death of those gaining a foothold in the early stages of succession, this territory is colonized by the grasses.

FIG. 21. *Calamovilfa gigantea* at the margin of a blow-out.

TRUE PRAIRIE

(*Stipa-Koeleria* Association)

The *Stipa-Koeleria* association has for its eastern limits the western border of the savannah. Much of this climax association, as a result of peculiar edaphic conditions, is occupied by the postclimax savannah. There is usually an abrupt change from grassland to savannah at the contact between the two communities. In contrast, the true prairie passes gradually into mixed prairie westward. This sharp transition in the east corresponds with a transition from hard to sandy soil, that in the west is entirely climatic. The western boundary of the true prairie is delimited approximately by a line running southwest from northeastern Grant County to western Tillman County. Thus, this association covers the Redbed plains and includes a

portion of the Gypsum-Hills region and the Wichita Mountains. The great annual fluctuations in precipitation and droughts are common and severe. Strong, desiccating winds are of frequent occurrence, the humidity is relatively low and water content often deficient. Such conditions are unfavorable to the growth of woody vegetation but favor the dominance of grasses. The consociations of the true prairie are: *Andropogon scoparius, A. chrysocomus, A. saccharoides, Bouteloua racemosa, Agropyron smithii,* and *Sporobolus asper.*

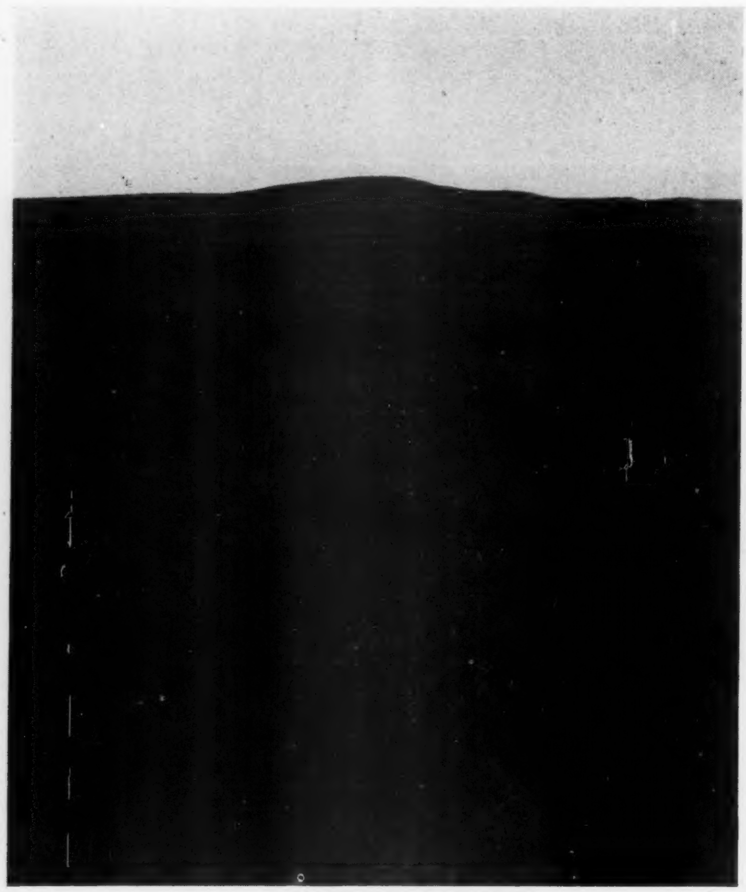

FIG. 22. *Andropogon scoparius* consociation of the true prairie.

The true prairie of Oklahoma is the southern portion of a grassland area which extends into Canada. It is characterized in this state by the *Andropogon scoparius* consociation, with *A. saccharoides* second in importance. *Stipa* and *Koeleria,* after which the association is named, are abundant and widely spread dominants farther northward but here are of relatively little importance. The little bluestem *(Andropogon scoparius)* is associated on the one hand with *A. furcatus,* and *A. chrysocomus* from the subclimax prairie

and on the other with elements from the mixed prairie and short-grass plains (Fig. 22). It is the principal sod-forming grass of the true prairie region and occurs over large tracts in almost pure stands. On the drier ridges of the true prairie or where heavily grazed, it ceases to be a sod former and assumes the bunch habit. Thus, under natural conditions, the appearance of short grasses in the sod of the true prairie indicates thin soil or other areas unusually low in water content; otherwise, it is a reliable indicator of over-grazing.

The bunches of *Andropogon scoparius* consist of only a few stalks or of large tufts containing as many as two hundred. The latter grow in size and frequently merge forming irregular bunches separated by small, bare spots and strips. In these unoccupied spaces, seedlings of subdominants gain a foothold and often become abundant. As the season advances most of the seedlings die as a result of the shade cast by the grasses which reduce their photosynthetic activity and especially because of the intense and unequal competition for water. After midsummer, the grasses obscure the bare areas and the prairie appears to be a uniform mass of waving foliage. In competition with the grasses, deeply rooted, society-forming plants absorb water from great depths (Weaver, 1920), and for a brief period spread their tops above those of the grasses. The development of such societies largely depends upon the excess of water and nutrients not used by the grasses (Fig. 23).

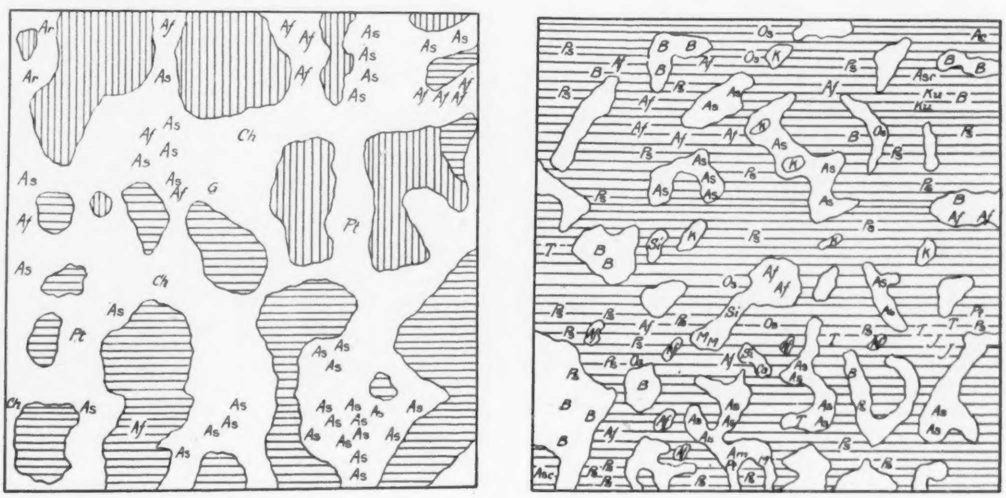

FIG. 23. Representative quadrats in the eastern part (left) and western edge of true prairie. Af or vertical hatch, *Andropogon furcatus;* As or horizontal hatch, *A. scoparius;* B, *Bouteloua racemosa;* the other plants are forbs.

Andropogon furcatus is common throughout the true prairie. It is an indicator of unusually high water content being largely confined to depressions and protected slopes. *A. chrysocomus* not only indicates a deep moist

soil but one containing considerable sand. It belongs typically to the post-climax prairie and where communities of it occur the true prairie conditions approach those of the region where it is the characteristic dominant. *A. saccharoides* occurs especially in the southern part of the true prairie. Its ecological requirements approach those of *A. scoparius* more closely than do those of either of the preceding grasses; in fact, it is a close ecological equivalent of *A. scoparius*. The fact that it commonly occurs on slightly disturbed areas, however, indicates that its water requirement may be somewhat greater than those of the latter, but it is found, as a rule, in habitats much too dry for *A. furcatus*.

Koeleria cristata and *Stipa spartea* occur only in scattered bunches in the true prairie. They never assume the rôle of dominants. Their scarcity is thought to be a result of overgrazing in spring and early summer.

Agropyron smithii is of common occurrence and is a local dominant in low, broad valleys or on gently rolling areas especially in the north central portion of the state. It is widely distributed throughout but forms consociations only locally. It forms a dense, tough sod.

Bouteloua gracilis, and *B. hirsuta* on sandy soils, form rather extensive consocies where the tall grasses have been suppressed by grazing.

Sporobolus asper occurs singly or in bunches of a few to a dozen stalks where the sod is rather open. It is not a sod-forming grass. In the spring and summer its harsh, dark green leaves are conspicuous among the other grasses but in winter its light color causes it to stand out against the background of the reddish brown bluestems.

Poa arida is a vernal blooming species of minor importance which occurs in clumps 1 to 6 inches in diameter. This grass is about a foot tall. It is conspicuous in May when it exceeds the height of the sod-forming grasses by several inches.

Tridens flava is a vigorous, rather tall grass which exhibits the bunch habit. The bunches are commonly 3 to 12 inches in diameter and 3 feet high. It is a common, interstitial species especially in more moist areas.

Aristida curtissii and *A. oligantha* are rather widely distributed. They occur where the soil has been disturbed and are important in revegetating denuded areas. They form bunches frequently about 3 or 4 inches in diameter.

Bromus secalinus, B. racemosus, and *B. unioloides* also frequent disturbed soils and overgrazed pastures. *Chloris verticillata* and *Eleusine indica* are weedy grasses frequently encountered where the native vegetation has been disturbed.

Societies

The vegetation of the true prairie is further characterized by the presence of numerous societies (Fig. 24). Because of the long growing season these

form prevernal, vernal, estival, and serotinal aspects. Bisect studies by Shantz (1911) and, later, the more extensive work of Weaver (1920) have shown that both the subterranean and aerial portions of the society-forming plants occur in strata not completely occupied by the grasses. Thus, competition between dominant and subdominant is greatly reduced.

Prevernal societies.[1]—Prevernal plants begin to make their appearance about the first of March, although such species as *Bursa bursa-pastoris, Draba caroliniana, Claytonia virginica,* and *Houstonia minima* may occasionally be found in protected places late in February. During March the prairie is characterized by *Erythronium mesachoreum, Nothoscordum bivalve, Anemone caroliniana, Androsace occidentalis, Antennaria campestris, Myosurus minimus, Sagina decumbens,* and *Viola rafinesquii.* The dominant grasses are at this time still dormant or just beginning to grow.

FIG. 24. Society of *Sabbatia campestris* in the true prairie.

The spring beauty *(Claytonia virginica)* is a low growing, bulbous, perennial which blooms four or five weeks in early spring and then, like many other prevernal plants, entirely disappears. The least bluet *(Houstonia minima)* is the smallest as well as one of the earliest plants of the prairie. In favorable seasons extensive carpets of green plants only an inch or two high are given a purple cast by their tiny but abundant purple-blue flowers. Two

[1] A complete list of societies of true prairie is deposited in the botanical libraries of the University of Nebraska and the University of Oklahoma.

crucifers, *Bursa* and *Draba*, are common, especially on barren spots. Another plant to appear in abundance is *Nothoscordum bivalve*, an alliaceous species strangely lacking the characteristic odor. It develops leaves 6 to 8 inches long and the flower stalks stand about 6 inches above the ground. This is just high enough to place the white flowers well above the foliage of the grasses which have developed a green background by the time it is in bloom. Moist situations on the prairie are frequently characterized by *Erythronium mesachoreum* which continues to bloom two or three weeks. The white flowered *Anemone caroliniana* appears abundantly on the prairies at about the same time. It is more common on rather dry south slopes and in pastures which have been closely grazed than it is in hay meadows where the growth of grasses is more luxuriant and the sod is less open. *Androsace occidentalis* is common on dry ridges but also occurs between the clumps of grasses in moister areas. The flower stalks, which are only an inch or two high, develop from tiny rosettes which appear in the fall and grow intermittently during the winter. The seed matures quickly and the plants are soon obscured by the growth of the vernal vegetation. The prairie cat'spaw *(Antennaria campestris)* forms grayish-green mats of woolly-pubescent plants which spring from stolons. *Antennaria plantaginifolia* also occurs about the same time, but it is less common. *Myosurus minimus* occurs in wet depressions on the prairie, while *Viola rafinesquii* and *Sagina decumbens* are found between the mats of the sod-forming grasses.

Vernal societies.—By late April or early May there is a well developed grassy carpet and numerous societies appear in rapid succession early in the vernal season. Perhaps the most conspicuous is *Baptisia bracteata*. The large, bushy plants stand well above the grasses and the great, drooping racemes of cream colored flowers contrast sharply with them. Later in the vernal season the less widely distributed *Baptisia australis* begins to bloom. It has a more erect habit of growth and the large, erect racemes of blue flowers frequently reach heights of 20 to 30 inches. *Baptisia sulphurea* and *B. sphaerocarpa* also occur but are more local in distribution and are found especially in the southern part of the state. *Senecio plattensis* with its orange-yellow inflorescence is abundant and conspicuous early in the vernal season. The umbelliferous *Cogswellia daucifolia* is quite abundant but due to its low habit of growth it is often somewhat obscured by the grasses. *Sisyrinchium graminoides* occurs in clumps often of 10 to 25 stalks, each of which grows 4 to 8 inches tall. Its grass-like appearance and bright blue flowers give it the common name of "blue-eyed grass."

Wild onions form extensive societies. Early in the vernal period *Allium nuttallii* appears and soon extensive communities characterize the drier, prairie soils. The societies are frequently so dense that other vegetation is obscured. After a brief period of blooming the plants rapidly mature and soon disappear completely except for their subterranean bulbs. *Allium*

mutabile later appears in the vernal period in more moist situations. In contrast to *A. nuttallii,* the societies are less extensive and individuals are more widely spaced. The plants are taller, however, and conspicuous because of the white, globose inflorescence. In the latter part of the vernal aspect, *Achillea lanulosa* makes its appearance. *Pentstemon cobaea,* with its glossy, green leaves and delicate, lavender-tinted flowers, is perhaps the most striking spring flower of the prairie. It is abundant on shallow, rather sterile soils. On deeper, fertile soils *Delphinium virescens* contributes to the beauty of the landscape by sending forth its tall, graceful racemes of grayish-white flowers.

Numerous species are also characteristic of dry, exposed clay or stony banks. Among them are the small, blue, liliaceous *Androstephium coeruleum, Yucca glauca, Evolvulus pilosus,* and 5 species of *Astragalus. Megapterium missouriense,* a gorgeous, yellow evening primrose, is a striking species of rocky soils because of its large flowers, red stems, and bright green leaves. It is conspicuous well into the estival period.

The transition from the vernal to the estival period is a gradual one. The vernal plants mature and more or less completely disappear while the serotinal golden rods, asters, and iron weeds and other autumnal blooming plants begin to make rather rapid vegetative growth.

Estival societies.—The beginning of the estival aspect is marked by the appearance of the white and yellow prairie clovers, *Petalostemon candidum* and *P. purpureum.* They are not the most imposing plants of the aspect but their complete absence from the vernal aspect and their wide range distinguishes them as characteristic societies. A little later, the less common *Petalostemon obovatus* with its yellow inflorescence is locally important. Milkweeds, many of which begin to flower in late spring, also characterize this aspect. *Asclepias tuberosa* is very abundant on slightly sandy soils. The plant has large leaves and conspicuous, orange-colored flowers. *Acerates angustifolia* and *Asclepiodora viridis* are common, especially in the early estival aspect, and later *Acerates viridiflora* and *Asclepias verticillata* also come into bloom. The pink flowered *Sabbatia campestris* and various species of *Croton* appear, among which *C. capitatus* and *C. texensis* are the most common. The various species of *Psoralea* are found everywhere and *Parosela enneandra* also is especially abundant throughout the true prairie.

In fact the psoraleas are probably the most widespread and characteristic society-forming plants of this aspect. They begin to bloom in the late vernal period and extend into the early portion of the estival. Their oval, green crowns, dotted with the purple alfalfa-like flower clusters, are lifted above the level of the grasses by slender, branching, herbaceous stems which break off near the ground when the plant matures. Thus the psoralea of early summer becomes a "tumble-weed" later in the season during the period of seed dissemination. *Psoralea tenuiflora* is the most common species; *P.*

lanceolata is similar and *P. esculenta* occurs in moist places. It does not characterize extensive landscapes as do the former species but the isolated individuals are somewhat hidden among the other vegetation of the moist places where it is usually found. *P. cuspidata* is common on rather sterile, rocky slopes and in such places is a conspicuous feature of the estival vegetation. Gauras are abundant both in number of species and individuals. Meibomias are less common but *Meibomia sessilifolia, M. paniculata,* and *M. illinoensis* are not infrequently encountered.

Drier portions of the true prairie are frequently characterized by societies of *Malvastrum coccineum, Ratibida columnaris, Plantago aristata,* and *P. purshii.* Infertile soils sustain societies of *Meriolix serrulata, Krameria secundiflora, Houstonia angustifolia, H. tenuifolia,* and *Hymenopappus* in the rather open grass cover.

Ravines and more moist places which have a more luxuriant grassy vegetation are commonly characterized by *Hartmannia speciosa,* a white-flowered evening primrose, *Lespedeza capitata, Glycyrrhiza lepidota, Silphium laciniatum, S. integrifolium,* and *Prionopsis ciliata.*

Other species characteristic of the latter part of the estival period are *Stenosiphon linifolium,* species of *Tithymalopsis* especially *T. corallata, Salvia pitcheri,* a common blue flowered mint which continues to bloom throughout the early serotinal period, *Meibomia canadensis,* and *Linum sulcatum.* The latter portion of the estival period is frequently so hot and dry that plants grow poorly.

Serotinal societies—The development of the serotinal aspect depends to a marked degree on the rainfall. In moist years the societies appear during August but if hot, dry weather prevails they develop more slowly and the characteristic autumnal aspect may be retarded until well into September. A number of plants begin to bloom in late summer and continue well into the serotinal season. *Croton, Dichrophyllum marginatum, Hieracium longipilum, Centaurea americana,* and *Amphiachyris dracunculoides* belong to this group. The goldenrods form the most characteristic autumnal society. They become conspicuous in August but reach their maximum development in September. *Solidago rigida, S. glaberrima, S. petiolaris, S. rigidiuscula, S. lindheimeriana,* and, in the drier places, *S. nemoralis* are characteristic species.

The blazing stars are also typical serotinal blooming plants, their purple spike-like inflorescences being common throughout the association. *Lacinaria acidota* and *L. punctata* frequent drier places but *Lacinaria squarrosa* and *L. pycnostachya* are more common where water content is higher. The hairy sunflower, *Helianthus mollis,* and *H. scaberrimus* are found abundantly among the grasses. In rather moist situations, as along streams and eroding banks, the more robust *H. maximiliani* and *H. grosse-serratus* are of frequent occurrence. The vernonias are widely distributed in the prairie but are usually most abundant in moist places. *Vernonia baldwinii, V. marginata,*

and *V. missurica* are representative. The asters mark the beginning of the serotinal aspect and are the last to disappear in fall. In favorable seasons, they may be found blooming in November long after the goldenrods, blazing stars, and most other species have matured and died.

MIXED PRAIRIE

(*Stipa-Bouteloua* Association)

The mixed prairie includes a large area of grassland lying between eastern Harper and Grant Counties in northeastern Oklahoma and extending southward to the Red River in the vicinity of Tillman County. In the central part of the state it reaches to the western border.

The eastern boundary is in contact with the *Stipa-Koeleria* association. On the west, its contact is with the short-grass plains. The Gypsum Hills escarpment has often been given as delimiting the eastern boundary of the short-grass plains (Fig. 25). Extensive studies have shown, however, that much of this area belongs to the mixed prairie. Definite boundaries are difficult to establish because of the broad ecotones between this association and

FIG. 25. Mixed prairie on the Gypsum hills in the central portion of the state.

the other grassland associations with which it is in contact. Much of it has been broken for agricultural purposes and the remainder has been subjected to such intense grazing that its composition has been greatly modified by the more or less complete elimination of the tall grasses from the mixture. Areas occur, however, where the vegetation has been protected from grazing and fires for long periods of time. The unusual rankness of the vegetation in such protected areas makes it seem doubtful if they present a natural as-

pect. Hay meadows and the right-of-way along railroads were assumed to have a flora which most nearly represented natural conditions. The following species are dominant: *Andropogon scoparius, A. saccharoides, Agropyron smithii, Koeleria cristata, Bulbilis dactyloides, Bouteloua gracilis, B. racemosa,* and *B. hirsuta.*

The mixed prairie is so designated because its dominance is shared by both tall and short grasses (Fig. 26). It consists of an upper layer of rather sparsely distributed tall grasses and a lower one of short grasses, or of alternating areas of tall and short grasses. The presence of extensive areas of *Agropyron* and *Stipa* explains the characteristic layering in the northern portion of the mixed prairie. In the south, *Stipa* and *Agropyron* as well as *Koeleria* become less abundant and the andropogons assume the most important rôle. The layers are well represented in Oklahoma where *Agropyron smithii* and *Bouteloua racemosa* are associated with *Bulbilis dactyloides,*

FIG. 26. Mixed prairie showing deciduous trees along the ravines and cedars on the rocky outcrops.

Bouteloua gracilis, or *B. hirsuta.* More commonly, however, *Andropogon scoparius* or *A. saccharoides* is associated with the short grasses (Fig. 27). Both of the tall-grass dominants are bunch formers but the short grasses form a sod in the intervening spaces. Zones and alternes result in which are found all degrees of mixing of the tall and short grasses.

Andropogon scoparius is one of the most widely spread dominants of the grassland formation. In the mixed prairie it assumes, for the most part, a

bunch habit and occurs typically as clumps more or less thickly scattered in a short-grass sod. Hence, it is commonly known as "bunch grass." The clumps are 6 to 12 or more inches in diameter and when the flower stalks are fully grown they reach a height of 18 to 20 inches. Dead flower stalks from the previous year's growth remain in the luxuriant green mats of the following spring. Early in the summer the reddish tinge characteristic of the andropogons appears and at maturity both flower stalks and foliage take on a reddish brown color.

Andropogon saccharoides is quite common in the southern part of the area where it forms clumps and in other respects is very much like the little bluestem. The white cotton-like bristles of the inflorescence make it easily distinguishable in the flowering stage. In habit it is less erect than *A. scoparius* and this tendency toward spreading helps in its identification during the vegetative stages.

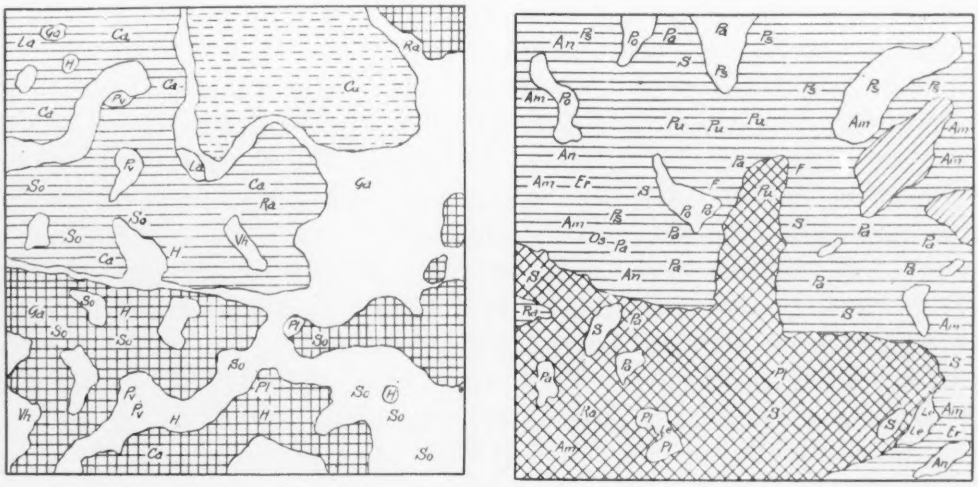

FIG. 27. Typical quadrats from mixed prairie. As or solid horizontal lines, *Andropogon scoparius;* Ari or broken horizontal lines, *Aristida purpurea;* Left hatch, *Andropogon saccharoides;* Bu or slanting cross hatch, *Bulbilis dactyloides;* Bg or vertical cross hatch, *Bouteloua gracilis;* Ps, *Panicum scribnerianum.* The other species are forbs.

Bouteloua gracilis is the most important single dominant. Its spread has been encouraged by grazing until it now extensively occurs throughout the area, frequently almost to the exclusion of other grasses. Under natural conditions it was probably much less abundant. It occurs as a codominant with all of the other dominants of the association. In the northern portion of the mixed prairie it is found with *Andropogon scoparius* and in the southern portion it is also frequently associated with *A. saccharoides.* It occurs locally with *Bouteloua racemosa,* and is found less frequently associated with *Bouteloua hirsuta* or *Bulbilis dactyloides* along with one or more of the tall grasses. Occasionally it is associated with *Agropyron,* especially in the north-

east. The most frequent grouping is formed with *Andropogon scoparius* and *Bouteloua racemosa*, accompanied by *Andropogon saccharoides* in the south.

Bouteloua racemosa probably reaches its maximum development in this association. It frequently forms consociations which almost exclude other species. Clipped quadrats in such communities gave yields of 200 to 250 grams per square meter. Pure stands are probably the results of rather local conditions since this dominant is more commonly found in associations with *Bouteloua gracilis* or *Andropogon scoparius*.

Bouteloua gracilis, the black or hairy grama, has a limited distribution since it is largely confined to dry, sandy soils. It abundantly occurs wherever the soil is too sandy for the other grasses to thrive.

Stipa spartea only rarely occurs in north-central Oklahoma. This may be a result of long continued grazing or due to the fact that it is a northern species which is approaching the southern limits of its range or, possibly, to a combination of these factors. It is included among the consociations because of its relation to the association as a whole. *Koeleria cristata* more commonly occurs but it does not form a consociation.

As a result of continued overgrazing many pastures almost entirely consist of the short grasses and a classification of the region as mixed prairie must take into account the history of the ranges. The vegetation in protected areas along lanes and highways presents indubitable evidence that the present condition of the grassland has been brought about by long continued grazing. *Andropogon scoparius* and other tall grasses are found in places where neither grazing nor mowing interferes with their development, but in grazed areas just across the fence hardly a spear of tall grass is to be found.

Rather extensive dune areas, which are occupied by *Andropogon chrysocomus* and the numerous species associated with this consocies on sandy soils, constitute the only important subclimax portion of the association. These sandy areas, into which the water deeply penetrates with little run-off or evaporation from the soil surface, form a habitat which supports a growth of vegetation comparable to that of moist regions farther east in the *Andropogon furcatus* consociation. The following grasses and sedges also occur here: *Aristida oligantha, Bouteloua texana, Bromus tectorum, Carex cherokeensis, Cyperus filiculmis, Distichlis spicata, Eragrostis curtipedicellata, E. purshii, E. secundiflora, Eriochloa punctata, Erioneuron pilosum, Festuca octoflora, Hordeum jubatum, Muhlenbergia racemosa, Munroa squarrosa, Panicum wilcoxianum, Poa arida, P. chapmaniana, Schedonnardus paniculatus, Sporobolus drummondii, S. texanus,* and *Tridens stricta.*

Societies

The societies of both mixed prairie and short-grass plains are found, with few exceptions, in the alternes of tall and short grasses that constitute the mixed prairie.

Prevernal societies.—In the areas intervening between the mats of sod, *Draba caroliniana, Sagina decumbens, Anemone decapetala, Androsace occidentalis,* and *Capnoides montanum* are found very early in the spring. A little later *Oxytropis lambertii, Allium nuttallii, Asclepiodora decumbens, Specularia leptocarpa,* and *Erigeron divergens* occur on moderately moist soil but the drier or more exposed places are characterized by *Antennaria dioica, Filago prolifera, Hoffmanseggia falcaria, Lappula texana, Myosotis virginica,* and *Lavauxia brachycarpa. Arenaria texana* and *Anogra albicaulis* occur on thin soil near rock outcrops and *Hymenoxys odorata* and *Townsendia exscapa* on dry eroding banks. The nodding violet *(Calceolaria verticillata)* occupies less exposed places.

Vernal societies.—During the vernal period numerous societies appear, many of which continue to blossom well into summer. Moderately moist prairies are characterized by *Indigofera leptosepala, Acuan jamesii, Chamaecrista fasciculata, Callirrhoe pedata, Linaria canadensis,* and *Acacia angustissima,* and the ravines by *Vincetoxicum cynanchoides, Tithymalus missouriensis, Pentstemon albidus,* and *Gaura sinuata.* Where the water content is lower, plants of a more xeric nature are found. Chief among these are *Plantago pusilla, P. purshii, Thelesperma gracile, Pectis angustifolia, Quincula lobata, Trepocarpus aethusae, Erigeron bellidiastrum, Chamaesyce lata,* and *Coryphantha missouriensis.* The following commonly form societies on dry rocky or gravelly soils: *Arenaria stricta, A. patula, Tetraneuris acaulis, Echinocereus caespitosus, Polypteris texana, Scutellaria resinosa, Coryphantha vivipara,* and *Chamaesaracha conioides.* Plants characteristic of eroding banks, etc., are *Solanum torreyi, S. triflorum, S. elaeagnifolium, Townsendia grandiflora, Eurytaenia texana,* and *Evolvulus pilosus.* Other common vernal species are *Castilleja sessiliflora* and *Malvastrum coccineum.*

Estival societies.—Species flowering in summer are for the most part deeply rooted and indicate the presence of moisture in the subsoil. Chief among these are *Amorpha canescens, Meibomia illinoensis, Oenothera biennis, Gaura coccinea, G. villosa, Meriolix serrulata, Allionia linearis, A. carletoni, Psoralea lanceolata, Stenosiphon linifolium, Bifora americana, Convolvulus incanus, Croton glandulosus, C. texensis, C. capitatus, C. monanthogynus, C. lindheimerianus,* and *Morongia uncinata.* The following are indicative of less favorable moisture relations: *Lygodesmia juncea, Asclepias pumila, Acerates angustifolia, Machaeranthera tanacetifolia, Petalostemon villosum, P. purpureum, Leptilon divaricatum, Amphiachyris dracunculoides, Mimosa borealis, Grindelia squarrosa, Linum lewisii, Leucelene ericoides,* and *Agalinis besseyana.* On dry, shallow or gravelly soil the following are sometimes found: *Othake callosum, Hymenopappus* sp., *Chrysopsis hispida, C. villosa, Sideranthus annuus, S. spinulosus, Opuntia polyacantha, O. tortispina,* and in the extreme southwest, *O. arborescens. Talinum calycinum, Portulaca pilosa, Psilostrophe villosa,* and *Verbena hastata* are characteristic of rocky

outcrops but on eroding banks, especially in the west, the following occur: *Melampodium leucanthum, Oreocarya suffruticosa, Meriolix capillifolia, Thymophylla aurea, Cryptantha crassisepala, Boebera papposa,* and *Nuttallia decapetala.* Other common societies of the mixed prairie are *Ratibida columnaris, Polygala verticillata, P. alba, Cirsium ochrocentrum, Hoffmanseggia jamesii, Prionopsis ciliata, Poteridium annuum, Gaillardia fastigiata,* and *G. lutea.* Rather late in summer *Eryngium leavenworthii, E. diffusum, Crassina grandiflora, Martynia louisiana, Paronychia jamesii,* and *P. sessiliflora* are conspicuous on dry soils. In more moist areas *Paronychia dichotoma, Physalis rotundata, P. lanceolata,* and *P. pumilia* occur. The following also are important: *Acerates angustifolia, Artemisia canadensis, A. frigida, Astragalus mollissimus, Mentzelia oligosperma, Nuttallia nuda, Phacelia integrifolia, Psoralea cuspidata,* and *Tragia ramosa.*

Serotinal societies.—Species characteristic of the drier prairies and plains in autumn are *Aster multiflorus, A. commutatus, Solidago nemoralis, S. radula, S. glaberrima, Otophylla densiflora, Agalinis aspera, Isopappus divaricatus,* and *Gutierrezia sarothrae.* Where the water content is higher the following usually occur: *Helianthus hirsutus, H. mollis, H. orgyalis, Heterotheca subaxillaris, Lacinaria squarrosa, L. punctata, Vernonia baldwinii,* and *V. marginata.*

Short-Grass Plains

(*Bulbilis-Bouteloua* Association)

The *Bulbilis-Bouteloua* association occurs only in extreme western Oklahoma. It includes the "panhandle," at least portions of the western tier of counties except Roger Mills and Beckham, and parts of other western counties. It is merely a continuation of the plains of Texas classified as the short-grass plains by Clements in 1916. It is also continuous with the plains of eastern Colorado where it was experimentally demonstrated that the dominant *Bulbilis* and *Bouteloua* represented the climax and that tall grasses are not able to establish themselves and reproduce in competition with the short grasses (Clements and Weaver, 1924). Shantz also classified it as short grass in 1924. The dominant species are: *Bouteloua gracilis, Bulbilis dactyloides,* and *Bouteloua hirsuta.*

The association is characterized by the complete dominance of the short grasses and by the absence of the tall grasses of the less xeric associations eastward. A dense sod completely covers the ground in level areas with soils of ordinary fertility and the slender leaves of the drought-resistant short grasses form a carpet 3 to 5 inches deep (Fig. 28). Soils that are thin, due to underlying rocks or gravel, support an open mat cover and bare areas are frequently extensive in the aggregate. Sharp differences occur between the northern and southern portions of the short-grass plains. The larger north-

ern area is typical short-grass country but the smaller southern portion is strongly modified by invasion from the desert scrub association.

The northern portion is characterized by the *Bouteloua gracilis* consociation or in the more moist portions by a *Bulbilis-Bouteloua* mictium in which the two short grasses meet on more or less equal terms. *Bouteloua* characterizes areas which have a drier soil and *Bulbilis* occupies those with higher water content. *Bouteloua hirsuta* frequently occurs with *B. gracilis* on somewhat sandy soils and *Aristida purpurea* may be found occasionally on deeper, less compact clays and loams.

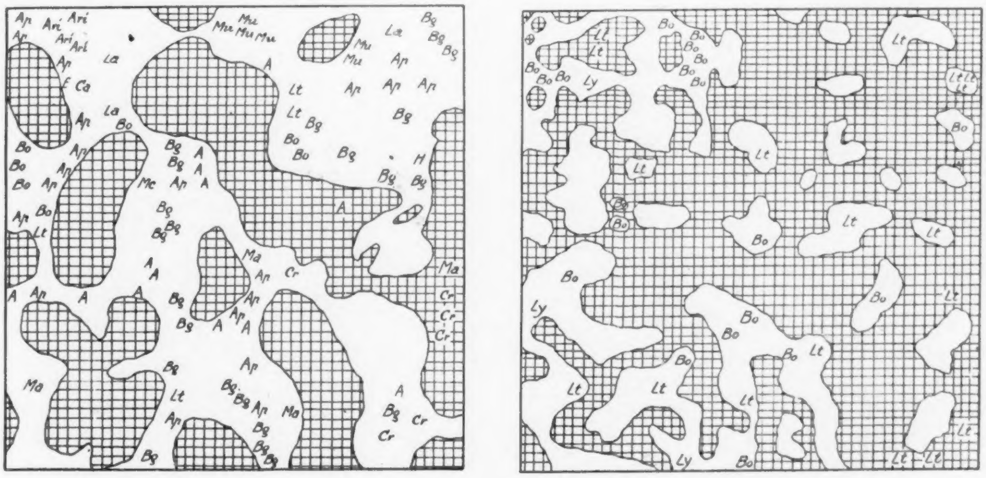

FIG. 28. Quadrats showing the open and closed type of sod formed by *Bouteloua gracilis*, (Bg or cross hatch). Some of the most abundant forbs are Bo, *Boebera papposa;* Lt, *Lappula texana;* and Ap, *Ambrosia psilostachya.* Other grasses are Mu, *Munroa squarrosa;* and Ari, *Aristida purpurea.*

The smaller, southwestern area centers in Harmon County and gradually merges into the mixed prairie. It is a continuation of the short-grass plains of Texas which lie westward and adjacent to the Texas mesquite and desert-grass savannah which borders it on the south. The short-grass cover is very open in the extreme southwestern part of the state but as the mixed prairie is approached a dense sod becomes characteristic. *Bouteloua gracilis* is the most abundant grass but *Bulbilis, Aristida,* and others occur. An effort was made to find the curly mesquite, *Hilaria belangeri,* and tobosa grass, *Hilaria mutica,* or other grasses which occur among the desert grasses or in the desert savannah. If present, they were not recognized in the drought-dormant condition which characterizes the vegetation much of the year.

Within a radius of about 30 miles from the southwest corner of the state, *Condalia obtusifolia* develops into large, thorny shrubs. These are frequently 6 to 8 feet high and 3 to 5 feet in diameter. They are widely and irregularly scattered over the short-grass ranges. Mesquite shrubs and trees abundantly occur, forming an open savannah of small trees 8 to 15 feet

high. The mesquite is abundant within a radius of 60 miles from the southwestern corner of the state and it also extends east to the Wichita Mountains and north to Woods County and the "panhandle" (Fig. 29).

FIG. 29. Mesquite *(Prosopis glandulosa)* in southwestern Oklahoma.

Yucca glauca is a common perennial associated with the grasses of both short-grass areas. It occurs in great abundance in the northern portion. The prickly pear cactus, *Opuntia lindheimeri,* forms numerous large mats, which are especially common in pastures (Fig. 30).

The region as a whole is characterized by the dense sod of the short grasses which form a carpet-like mat of foliage that is interrupted but little by trees, shrubs, or tall grasses even in the moister parts. The tough, fibrous roots and rhizomes bind the soil and protect it from water erosion just as the mat-like cover of leaves retards the erosive effects of torrential rains and wind.

Bouteloua gracilis forms the most extensive and important consociation (Fig. 31). It also extends as a codominant throughout. It may be found associated with any of the dominants but most frequently with *Bulbilis.*

Characteristically, it forms a dense sod except on thin, stony soil. Its ability to become dormant during drought and resume growth upon the advent of rain remarkably adapts it to its environment. It is of great economic importance as forage due to its palatability and to the fact that it "cures" naturally and furnishes excellent winter grazing.

Bulbilis dactyloides, like the blue grama, rapidly develops after rains and retains its nutritive qualities when dry but it requires a slightly more moist habitat. It is found in slight depressions or in areas which for other reasons have a somewhat higher water content. It is commonly associated with slender grama but rarely with other dominants in the absence of *Bouteloua*.

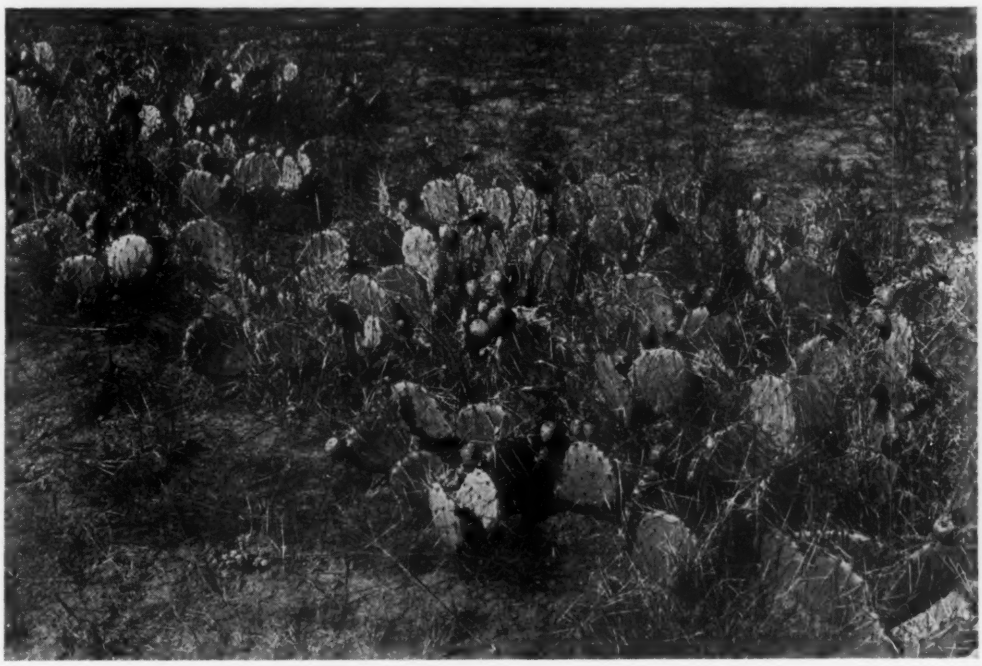

FIG. 30. *Opuntia* on an overgrazed western prairie.

Bouteloua hirsuta is third in importance. Its range is less extensive than that of the other short grasses. Its presence indicates a comparatively open soil.

Bouteloua racemosa is an important associate of the short grasses near the eastern border of the Great Plains and on sandy areas. Its low growth-form enables it to withstand a considerable degree of grazing. The broader leaves and taller habit of growth makes it easily distinguishable from the short grasses and when the flower stalks have developed it is conspicuous even at a distance. The continual close cropping reduces the size and vigor of the plant until its leaves frequently do not exceed in height those of the

short grama grasses with which it is frequently associated. Its abundance eastward indicates the transition to mixed prairie.

There are two important postclimax types of vegetation found within the boundaries of this association. Both occupy sandy tracts of land, frequently of considerable extent, which are usually dunes. The subclimax *Andropogon* prairie is similar to that already described for the sandy areas of western Oklahoma. Sand sage, *Artemisia filifolia,* also occupies extensive areas and is usually associated with tall grasses and other plants which indicate its postclimax nature. Grazing has almost exterminated the grasses and an almost complete cover of sagebrush has developed. These shrubs are rather uniformly 3 to 4 feet high and develop a more or less spherical crown.

Fig. 31. *Bouteloua gracilis* on the high plains of western Oklahoma.

Societies of the short-grass plains are similar to those of mixed prairie, although less abundant and more poorly developed. Many of the less xeric species of mixed prairie do not occur, but a few xeric species from the southwest not found in mixed prairie are present. Where the grassy cover is dense the sod prevents water penetration to levels from which the deeply rooted, society forming species absorb and only a few xeric societies are able to exist. Only where the short-grass cover has been disturbed as a result of grazing or by erosion and water penetrates to deeper levels are societies at all abundant.

Relative Plant Production in Grasslands

The different climatic conditions under which the several prairie communities occur is clearly reflected in total plant production (Weaver, 1924). By

using clipped quadrats, the plant community becomes a type of phytometer. Plant production as measured by dry weight is one of the most significant methods of integrating differences in habitat. Practically all of the measurements in the ecological analysis of habitats are primarily concerned in evaluating the several conditions for plant growth.

The method employed was to select five or more quadrats typical of each community after a careful study had been made as to composition, density, and kind of vegetation. One or more of these was then clipped near the ground by means of hand shears and the plants secured in cheesecloth bags. This procedure was then repeated in other, distant portions of the same community until about 15 representative clippings were secured. The plants were dried in the sun, and all clippings finally accumulated in a laboratory at the University of Oklahoma where they were equally air dried and weighed.

Fluctuations in dry weight within a community are due in part to the differences in the structure of the vegetation and in part to the time of cutting. All of the quadrats were clipped during 1926 and after the foliage was fully developed to the time of complete flower-stalk production. The flower stalks greatly increase the dry weight. The summer of 1926 was one of abnormally high rainfall. The average increase above the mean was 6 inches with some stations reporting 10 to 16 inches above.

Summarizing, the average yield from the subclimax prairie was 760 grams (range 367 to 1478) under a mean annual precipitation of 40 inches. The true prairie, with a rainfall of 30 inches, gave an average yield of 507 grams (range 290 to 823). Westward in the mixed prairie, with a decrease in rainfall to 25 inches, the average yield was 393 grams (range 215 to 450). Plant production in the short-grass plains was only 182 grams per square meter (range 69 to 301) under a rainfall of 20 inches or less.

SUMMARY

The state of Oklahoma is 470 miles long and 225 miles wide. It consists of a plain which slopes from the northwest to the southeast and includes portions of eleven physiographic provinces, four of which are mountainous.

The area is drained by the Arkansas and Red River systems. These rise in the Rocky Mountains, enter the state from the west, and flow in an easterly or southeasterly direction.

The annual precipitation varies from 45 inches in the southeast to about 20 inches in the northwest. The major portion of this falls during the growing season. In central and western Oklahoma long periods of drought occur. These are accentuated by a high rate of evaporation and high wind velocity.

The soils are extremely variable as are also the underlying rocks from which they have mainly originated.

Owing to the wide range in latitude and altitude and its effect upon precipitation, as well as the diversity in topography and soils, a variety of conditions is presented for the growth of plants.

The oak-hickory association extends into the eastern part of the state from Arkansas and in general occupies the Ozark and Ouachita Mountains. On the poorer soils of the southeast, a northern outpost of the southern coniferous forest is represented by a consocies of *Pinus echinata*.

The oak-hickory savannah lies west of the deciduous forest and, except for a large lobe of the subclimax prairie entering from the north, occupies sandy and rocky soils as far west as central Oklahoma. Here woodland and grassland form extensive alternes. The flood-plain forest consists of numerous, well developed associes in the east. Miniature swamps of *Taxodium* also occur. In central Oklahoma many of the eastern species are not found and westward only scattered groups of poorly developed trees occur.

The subclimax chaparral (*Rhus-Quercus* associes) forms the ecotone between the various forest communities and the bordering grassland.

The *Andropogon* associes occupies a large area in the northeast which separates the oak-hickory climax from the oak-savannah. Numerous other isolated postclimax areas occur on sandy soils in the west.

The true prairie (*Stipa-Koeleria* association) extends north and south across the state west of the savannah. The mixed-prairie (*Stipa-Bouteloua* association) lies still farther westward in a region of lower precipitation and greater evaporation. The short-grass plains (*Bulbilis-Bouteloua* association) is represented in the "panhandle" and in a narrow belt in the northwestern part of the state. Because of extremely xeric conditions, tall grasses are absent and only short grasses and a few xeric societies occur.

As the moist climate of eastern Oklahoma becomes gradually drier westward, mesic communities are replaced by xeric ones. There is a change in growth-form; and the rate of growth of woody plants along streams is gradually decreased. There is also a marked decrease in the total yield of the grasses.

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THE MEASUREMENT OF DAYLIGHT IN THE CHICAGO AREA AND ITS ECOLOGICAL SIGNIFICANCE

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CONTENTS

THE MEASUREMENT OF DAYLIGHT IN THE CHICAGO AREA AND ITS ECOLOGICAL SIGNIFICANCE

Introduction

Radiant energy is probably the most important single factor governing the activities of organisms, in so far as any one factor is capable of exerting an independent effect. Bayliss (1924, p. 548) discussing the action of light, voices the common conclusion that "the whole existence of living organisms on the earth depends on the receipt of radiant energy from the sun. . . ." The action of radiant energy, due to its complex physical nature, may not be attacked as a whole. Rather, biologists have found it both necessary and convenient, so far, to divide radiant energy into three separate factors, *viz.* heat, light, and ultra-violet radiation, and each of these has been further subdivided. It is to be noted here that, notwithstanding the different effects of these factors on organic activity, they are closely related portions of the same physical category. Indeed, the portions of the spectrum differ quantitatively, in wave length and frequency, rather than qualitatively. Consequently, any biological philosophy, aiming at completeness, should take into account this basic interrelationship.

The components of radiant energy have received differential attention. The measurement and significance of heat, with respect to plants and animals, has been extensively investigated in the past; work upon ultra-violet radiation is the most recent in its development and of necessity requires special technique, and its ecological significance largely awaits investigation. The study of light, so called, or more properly, visible radiation, is also as yet in an unsatisfactory state as far as the knowledge of its action on living things is concerned; even the quantity of light received in different natural habitats has been but little investigated. The measurement of light as an ecological factor in the land habitats has been studied for little more than twenty years. Warming (1909) discussed the importance of light and heat in relation to plants, placing emphasis upon the latter factor. With respect to light he enumerated the various ways in which radiation played a part, distinguished between sun-plants and shade-plants and found light to be "one of the most important factors influencing transpiration. . . . But for further information in this matter we must look to the future."

Light has been long recognized as an important factor in the life of the higher plants, and recent general works on animal ecology (Chapman, 1926; Pearse, 1926; Elton, 1927) have enumerated how light is, or may be of importance for animals. In the last quarter of a century, however, the study of the effects of light upon laboratory animals has been more often pursued than the study of light as a factor in the natural habitats. The desirability

of the latter is becoming evident. "One important physical factor that has hitherto been grossly neglected in environmental studies is that of light" (Allee, 1927, p. 441).

The observations described in this paper have as their object the answering of two general questions:—(1) what is the intensity of daylight in the Chicago area, with special reference to the upland forest-on-sand sere; and (2) of what importance is light in the study of community ecology?

The writer takes pleasure in acknowledging the coöperation of several professors in the University of Chicago: especially to Dr. W. C. Allee, of the Department of Zoölogy, am I indebted for untiring advice and criticism; Drs. H. C. Cowles and G. D. Fuller, Department of Botany; to Dr. G. S. Monk, Department of Physics; to my field companions, Dr. J. H. Davis, Jr., Dr. C. Sandstrom, Mr. J. P. E. Morrison, and Mr. H. S. Denninger, and to Mr. J. A. Maxwell of the Pilcher Arboretum, Joliet, Illinois. Information has been given by the Leeds and Northrup Company, and the Electrical Testing Laboratories, Mr. P. E. Johnson of the University Observatory, and Mr. Whitney of the Chicago Weather Bureau.

1. The Nature of Daylight

Before proceeding with an analysis of the data, some mention should be made briefly of the factors modifying daylight intensity. The spectral character of daylight has been neglected in ecological habitat studies, and the field measurement of this factor has been made only recently practicable (Klugh, 1930), therefore a careful discussion of ultra violet is not attempted. The ever changing nature of daylight is found to be complex. By "daylight," Luckiesh (1922, pp. 15-16) understands the general result of three forms of radiant energy, (1) direct solar radiation, or "sunlight," (2) diffuse sky radiation, or "skylight," and (3) radiation variously reflected from trees, or other objects of the environment, which is largely dependent upon the various reflection and absorption values of these objects. Thus overcast days may reduce direct sunlight to zero, while on clear days the total light incident on a horizontal surface is composed of about 10% skylight and about 90% direct sunlight. On very clear days the amount of skylight may be as much as 20%. In general the amount of direct sunlight varies inversely with the amount of skylight.

Solar radiation is known to vary with the condition of the atmosphere, e.g. dust or other particles, amount or nature of water vapor present, with altitude, latitude, time of day, and time of year. The incident energy varies from season to season and moment to moment sufficiently to cause as much as a five per cent difference in the solar constant. The latter may vary about the mean of 1.93 calories per square centimeter of horizontal surface per minute, within the limits of 1.8 to 2.0 calories throughout an average year. This means that energy is received approximately at the rate of .16 horse

power per square foot, or about 7000 horse power per acre. An extensive literature has been developed upon this subject. Solar periodicity and the solar constant have been investigated by a host of workers, of whom may be mentioned Abbot (1921, 1923), Abbot and Fowle (1908, 1911), Angström (1922), Clayton (1925), Kimball (1924, 1924a), Knott (1903), Marvin (1923), Poynting (1904), Very (1901, 1911).

With change in solar radiation, from moment to moment, there is a change in the photochemical activity of sunlight, a fact to be noted for proper comprehension of the effects of radiation. The intensity of light is appreciably cut down by atmospheric absorption and atmospheric scattering. Clear days may have an atmospheric absorption of over 25% (Luckiesh in Cady and Dates, 1925, p. 337). The effect of atmospheric scattering on incoming radiation may be marked, since there is appreciable matter in the air at an altitude of from 50 to 100 miles. Atmospheric scattering is treated adequately by Very (1900, 1901a), Humphreys (1920, pp. 538-555), and by Fowle (1921). Luckiesh (1922, p. 16) finds the daylight intensity in the United States to be generally 10,000 foot-candles on clear, midsummer days. On clear to hazy days the illumination due to skylight usually falls between 1000 and 2500 foot-candles. On clear midwinter days the total intensity may average around 2000, and on cloudy days sink to 1000 foot-candles, or less. In addition to clouds, the presence of smoke will greatly reduce daylight intensity. Luckiesh (Cady and Dates, 1925, p. 337) states that "in industrial districts the intensity falls to only a small fraction of that found in the country on the same day." The effect of fog on daylight intensity has been investigated by Unger (1923) among others, and Kimball and Hand (1925) have worked on the effect of dust in the atmosphere.

Luckiesh (Cady and Dates, 1925, p. 338) assigns the following percentages of light reflected by earth areas, "as determined by viewing vertically downward," as follows:

Woods	4.0%
Barren ground	13.0%
Fields	7.0%
Inland water	7.0%
Deep ocean water	3.5%
Dense clouds	78.0%

Pulling (1919, p. 169) observed that fog clouds, by reflection, reduce solar radiation 65%, and Aldrich (1921), using a pyranometer suspended from an army observation balloon, found the mean reflection value of a level cloud surface to be 78%. Thus it will be seen that the study of clouds is important to understand the action of daylight. The work of Humphreys (1920) and of Clayden (1925) should be mentioned in connection with cloud study. Numerous investigators have studied monthly and annual mean cloudiness, and duration of sunshine as measured in various units. Reed (1923) gave general data for Central America. Kimball (1914) used

a Sharp-Millar photometer and measured daylight intensity at Mount Weather, Virginia. Kimball and Hand (1921) with the same type of apparatus compared the radiation at Washington, D. C., with that at Chicago, Illinois. These authors in a later paper (1922) dealt especially with illumination on horizontal, vertical, and sloping surfaces (see also Kimball, 1925a).

Kimball (1924, p. 473) found that "comparisons between photometric measurements of daylight and pyrheliometric measurements of the total solar radiation lead to the same result. They indicate, however, that if the radiation intensity on a horizontal surface, expressed in gram-calories per minute per cm., is multiplied by 6700, the result will give the illumination intensity on a horizontal surface in foot-candles within $\pm$ 5 per cent, giving values which near noon are too low and which are too high when the sun is near the horizon." Further, Kimball (p. 479) found that when the sky is covered by clouds the factor will average higher, probably not far from 7000. The formula given, viz, Gm. Cal. / $cm.^2$ / min. x 6700 foot-candles, gives a ready check for photometric measurements or vice versa, and also makes available a great amount of data for biological investigation.

In summary, Pulling (1919, p. 169) notes seven chief ways in which solar radiation coming to the earth may be modified: (1) general scattering by permanent gases of the atmosphere; (2) general scattering by water vapor; (3) selective (banded) absorption by the permanent atmospheric gases; (4) selective (banded) absorption by water vapor; (5) absorption and reflection by clouds; (6) absorption and reflection by dust; and (7) absorption by chemical reactions. From this brief account it will be seen that daylight, as admitted to a given habitat and especially to the forest floor may be profoundly modified both in its intensity and spectral composition by many different factors. Conclusions, then as to its effect upon organic activity should be reached with caution, especially when, as at present, only intensity data are available for the communities observed. These same communities have been studied intensively by Cowles (1899, 1901), Fuller (1911, 1912, 1912a), Shelford (1913), and their students. A brief summary of these ecological investigations in the Chicago Area has been published by the writer (Park, 1931, 1931a).

2. Statement of Conditions and Methods

In an attempt to correlate daylight with animal distribution in the upland forest sere, the intensity of light penetrating to the floor was measured in foot-candles with a Macbeth Illuminometer. This apparatus has been fully described in a bulletin of the Leeds and Northup Company (1925). It is a "comparison photometer," measuring visible radiation in terms of foot-candles and depending upon an ocular comparison of the light to be studied with a light of known luminosity. A discussion of comparison photometers is given by Zon and Graves (1911), Pulling (1919), Bates and Zon (1922) and Klugh (1925).

The Macbeth Illuminometer has been criticized by Klugh (1927, p. 417), "For artificial illumination it is an ideal instrument, but when one is concerned with daylight, and with light of a distinctly 'blue' character, as that from the blue sky in the woods, the difficulty of matching the intensity of the yellow field of the comparison lamp against the blue field of the habitat is a very real one. Many experiments with filters of various kinds were carried out, and, much to my disappointment, it was found that no combination of filters permitted the accurate measurement of light of different spectral qualities." The writer has not been concerned with an analysis of the different spectral qualities of daylight in the present study. No extraordinary difficulty has been experienced in matching the daylight received with the artificial source when the appropriate gelatin filters were used and the instrument standardized to the observer's eye against the reference standard lamp. It should be remembered that the light measured with the Macbeth Illuminometer was that falling on the porcelain test plate, a known part of which was subsequently reflected into the telescope of the instrument, and that such measurement does not necessarily register that actually reflected from the floor, and does not show the light that would affect an animal in the same habitat. Thus the rounded eyes of, say, a beetle would be exposed to light rays falling from above, whose intensity would be measured by the Macbeth Illuminometer, as well as that reflected from both sides and the floor of its environment, which this instrument, as used here, did not record. The Macbeth Illuminometer has been used previously in ecological studies by Weese (1924) for a limited series of observations in an Illinois elm-maple forest, by Allee (1926) for several weeks in the rain forests of Barro Colorado Island, Panama, and recently by Grasovsky (1929) in an investigation of the rôle of light in forest reproduction; the instrument is discussed by Shelford (1929, pp. 339-342).

In the present study, beginning with April, 1922, and extending through December, 1928, 243 field trips have been made in the upland forest-on-sand sere of the Chicago area (Park, 1930, 1931). Between March, 1926 and September, 1929, 83 days were spent in the field measuring daylight intensity, or an average of 2.44 days per month so that sufficient time has been used to obtain some indication of the daily and seasonal distribution of daylight in a series of genetically related communities. Determinations of daylight intensity were made in unshaded areas (designated as unobstructed sun); and in the pioneer cottonwood, conifer, black oak; oak-elm subclimax; beech-maple and maple climax communities of this upland forest-on-sand sere, and in addition, in a number of intermediate forest associes, which have been described by Cowles (1899, 1901). Due to geographic extent, the pioneer communities of the dune area (along the shore of Lake Michigan, from Tremont, Indiana to Gary, Indiana) were visited one day, and the climax communities (beech-maple at Lakeside, Michigan and Michigan City, Indiana,

and maple at Pilcher Arboretum, Joliet, Illinois) on another day, the trips covering this area being made as close together as circumstances permitted.

Since the daylight as received by the forest floor was not the same at any two moments on account of a variety of causes mentioned previously, the value of these ever-changing intensities depended upon comparison, with the least delay possible, with the intensity of the unobstructed sun. Open spots, clearing or unshaded meadows were visited for this purpose. Sun flecks on the floor were not used as comparison standards, since the light penetrating through the interstices of a canopy is subject to reflection and interference by leaves and branches, and is in part absorbed differentially, so that the resulting sun fleck is quite generally much lower in intensity than unobstructed sun, despite its relatively brilliant appearance. In the communities studied, both sporadic readings over the floor and regular stations in each typical associes were made. In all cases, however, the intensity was measured as falling on the floor from foliage or branch canopy shade, care being taken to omit, when possible, the more constant shade cast by trunks or large limbs. Such readings were attempted, then, which would present the typical shade cast from the canopy of the characteristic or dominant trees of each associes. In as much as the heavy trunk shade was neglected on the one hand, the light periphery shade was likewise omitted, or the two averaged together to give the mean value. Under the conditions obtaining, however, it was found that a given community would present an average intensity of daylight, at a given time of the day and year, so that by the accumulation of data, average expressions of daylight intensity could be built up. In all save a few cases, the great majority of readings were made on, or within four inches of the forest floor. The test plate was kept clean and in as horizontal a position as possible. Although the time spent in the field varied from trip to trip, the usual period spent in measuring daylight intensity was eight hours, from eight in the morning to four in the afternoon, central standard time.

3. DATA ON DAYLIGHT INTENSITY

Tables I, II, and III summarize the measurements of daylight intensities as received on the forest floor for the period mentioned previously. Table I shows the hourly means for the unobstructed sun in foot-candles for 1926, 1927, and 1928. The figures for any day so listed are compiled from the original field records. It should be noted that some of the readings are apparently unusually high in value, e.g. June 19, 1926. Such relatively high intensities, however, were probably due to inexperience in using the Macbeth Illuminometer, viz. failure to match the illuminated circles accurately, or to properly standardize the instrument against the reference standard cell. This is further indicated by the fact that similarly high readings are not found for 1927-1928 of the table. On the other hand June 19, 1926 was a very

TABLE I. *Unobstructed Sun in Foot-Candles*
(Central Standard Time)

Date	A. M.				P. M.				
	8–9	9–10	10–11	11–12	12–1	1–2	2–3	3–4	4–5
1926									
May 5	......	9818.97	754.74	......	......	8644.8			
May 7	7545.5	......	7604.55	......	......	6830.4	3964.6		
May 11	......	13180.2	14087.8	......	14514.8				
May 15	......	9605.3	1877.2	......	8217.9	......	6937.2		
May 17	1892.8	8893.8	3842.1	10743.7	......	8804.9	1059.4		
May 21	......	......	1915.6	3964.15	7524.21	......	9590.2		
May 24	7831.09	......	9569.8	......	11597.61	5111.99			
May 29	8538.2	10601.49	......	11152.91	......	9477.3	6262.58	5026.81	
June 2	8004.0	10245.7	10492.8						
June 9	8466.9	12807.1	13269.6	13234.08	......	13162.9	11900.2		
June 13	......	800.37	1451.29	7745.61	......	8164.5			
June 19	......	......	......	......	14941.71	15048.4	16169.0	9605.38	
June 25	9231.8	12700.4	12807.1	12807.1	......	13701.6			
July 1	......	2732.6	2942.8	2690.63					
July 10	......	6688.18	......	4254.6	3948.87	2303.66			
July 14	......	......	......	14187.76	......	13447.53			
July 16	......	11099.55	......	11099.5	12237.9	11882.21	......	9605.38	
July 23	......	......	......	11750.6	13767.7	10352.4	......	6617.04	
Sept. 11	......	......	11611.84						
Nov. 27	......	......	......	......	......	......	230.64		49.3
Dec. 19	......	......	......	......	208.5				
Dec. 30	......	......	......	......	......	1693.4	1441.57	989.04	
1927									
Mar. 16	......	......	3855.04	5907.04	......	......	4756.94		
Mar. 29	......	3419.2	2431.2	2186.1	1345.32				
Mar. 31	......	3251.1	3167.1	2690.6	2522.4				
Apr. 4	......	4240.2	2522.4	1855.6	1775.1	3237.1	3363.3		
Apr. 6	......	7630.9	7257.4	8644.7	7648.7	5976.6	6403.5		
Apr. 18	......	......	......	......	......	1305.52	......	437.2	
Apr. 20	......	6681.0	8506.4	5336.3	6190.1				

TABLE I. *(Continued)*

Date	A. M.				P. M.				
	8–9	9–10	10–11	11–12	12–1	1–2	2–3	3–4	4–5
Apr. 23	......	......	......	7719.88	......	8804.93			
Apr. 26	4567.4	5827.2	......	7916.8	9712.1	9605.3			
May 2	672.6	1670.4	......	1250.0	2270.2	2386.6			
May 4	2909.8	2146.9	1188.3	......	1702.6				
May 11	672.6	689.4	803.8						
May 17	......	3855.49							
June 2	......	......	3711.7	......	......	640.59			
June 7	......	6319.7	......	......	1479.85				
June 9	7115.09	......	8502.54	......	8751.57	7684.3			
June 17	......	......	6937.22	......	8075.6				
June 22	......	......	......	9178.4	9178.4	9178.4			
July 12	3195.12	......	6322.63	......	8182.36				
July 23	......	......	......	......	14941.7	12807.1			
July 26	......	......	......	13800.6	12558.1	13091.7	7172.0	5941.1	2909.9
Sept. 11	......	9946.9	10601.4	13376.3	11455.3				
Oct. 13	......	......	......	......	1069.52	225.33			
Oct. 15	......	10672.6	13483.1	16062.3	15155.1				
Oct. 16	......	......	......	......	......	......	10192.37		
Oct. 22	......	10530.3	12166.8	12251.4	......	8004.48			
Oct. 27	......	8395.8	......	10512.55	......	......	8751.51	3111.05	
Nov. 3	......	3867.5	3237.1	3054.9	1723.6	10288.4	9391.9	2646.8	
Nov. 10	......	......	565.74	......	......	......	521.3		
Nov. 24	......	155.88	......	1044.48	1420.05	1042.62	165.77		
Dec. 10	......	......	......	1681.6	1513.4	3007.6	400.47	289.67	
Dec. 14	......	......	......	......	......	......	2817.57	2438.39	
Dec. 24	......	......	2060.0	2438.39	......	4556.76			
1928									
Jan. 5	......	......	......	4269.06	7043.94	5772.01	1807.77		
Jan. 10	......	......	......	8965.02	9036.17	......	5620.9	1807.77	
Jan. 31	......	6168.7	8111.2	7328.5	......	6723.7	......	950.12	416.2
Feb. 28	......	6211.4	9889.9	5282.9	13020.1	10290.7	9818.8	7043.9	2690.6

TABLE I. *(Continued)*

DATE	A. M.				P. M.				
	8–9	9–10	10–11	11–12	12–1	1–2	2–3	3–4	4–5
Feb. 29	......	2858.8	3447.3	3909.8	6510.8	8164.5	4312.6	6190.1	810.5
Mar. 24	5443.0	9178.4	4287.1	8255.5	7470.8	3628.7	4624.8	306.02	
Mar. 31	......	6474.7	7684.3	10672.6	10672.6	9567.8	7043.9	4055.6	975.3
Apr. 21	......	......	......	1649.4	5661.6	9400.3			
Apr. 25	......	......	7904.8	8973.1	9614.0	10254.9	8118.5	......	3204.6
Apr. 26	......	5768.4	7103.7	8545.8					
Apr. 28	......	......	7477.5	8973.1	8545.8	4807.0	6249.1	4272.9	3845.6
Apr. 29	4379.7	1531.6	7904.8	3113.8	6249.1	3702.9	5554.7	4486.5	450.2
May 12	6836.6	8011.6	7947.6	8118.5	9186.7	8225.3	7157.1	5768.4	4326.2
May 22	6836.6	7050.2	7904.8	8545.8	8545.8	7904.8	6729.8	5554.7	4593.3
May 23	6309.5	......	6516.1	7691.2	8118.5	......	5982.0	4913.8	3375.5
May 26	......	8438.9	10148.1	......	......	900.48			
June 14	6195.7	7952.9	7477.5	7477.5	7691.2	7584.4	8011.6	6049.3	3311.4
June 15	6622.9	8338.9	8335.5	7904.8	8225.3	......	7157.1	6195.7	5554.7
July 29	3525.1	5341.1	6336.6	5127.4	6409.3	5715.0	5715.0	......	2230.1
1928									
Aug. 8	6088.8	6729.8	8332.1	......	7765.7	7691.2	......	3738.7	1851.4
Aug. 10	4166.0	......	6409.3	8438.9	8118.5	......	5768.4	2991.0	2136.4
Aug. 14	......	......	6979.0	......	11964.1	13032.3	......	10682.2	
Aug. 22	......	6623.0	8866.2	9614.0	8545.8	8118.5	7691.2	6836.6	4913.8
Aug. 24	......	7014.6	......	7833.6	8252.0	7263.9	6623.0	5234.3	3418.3
Aug. 31	......	......	......	......	10735.6	8278.7	6623.0	......	3418.3
Sept. 23	......	......	9186.7	9507.2					
Sept. 24	2563.7	2608.8	6409.3	2956.0	......	740.59	......	1312.8	866.8
Sept. 25	......	......	......	......	......	5346.1	......	......	2482.6
Sept. 26	......	......	......	3418.32					
Sept. 29	......	......	6623.0	......	......	4913.8	3508.9	1464.3	1481.1
Sept. 30	3029.6	......	5875.2	7477.5	8118.5	7263.9	......	4379.7	1683.1

TABLE II. *Cottonwood Associes*

Similar data are available for other years in this associes and for the other associes studied; see text.
(Lake Michigan Dunes, especially Long Lake and Ogden Dunes, Indiana)

DATE		A. M.				P. M.				
	7–8	8–9	9–10	10–11	11–12	12–1	1–2	2–3	3–4	4–5
1926										
May 7		......	......	2582.4	......	......	4191.3			
May 5		......	......	6883.8						
May 11		......	3267.12	......	5697.87					
May 17		......	......	......	1391.43	......	2876.46			
May 24		......	......	2190.55	......	2827.04				
May 29		......	1014.89	......	1614.45	......	......	1345.32	1435.0	
June 2		......	......	891.27						
June 9		......	682.86	......	950.22					
June 19		......	......	......	......	......	......	1035.61		
June 25		......	......	1807.77	......	2025.27				
July 10		......	......	......	2294.24	930.51				
July 16		......	......	......	......	1676.6	1664.8	1959.1		
July 23		......	......	......	......	......	......	......	472.95	
Sept. 11	316.1	......	......	380.41						
Nov. 27		......	......	......	......	......	......	......	37.1	

TABLE III. *Summation of Daylight Intensity in the Chicago Area, Given in Foot-Candles*

The following table is a summation of the hourly means of the days spent in the field. These readings have been calculated twice and are accurate to plus or minus 25 foot-candles.

Year and Month	Associes				
	Open Sun	Populus	Pinus	Quercus	Acer
1926					
May	7580.70	2101.35	888.58	1681.24	537.89
June	10562.90	1296.16	730.96	429.46	122.88
July	8422.73	1499.71	922.77	531.80	152.62
September	8527.44	348.25	......	107.31	
November	230.64	37.10	27.89	103.65	
December	1333.12	......	......	......	288.39
1927					
March	3230.29	1482.89	430.01	1374.59	1393.08
April	5686.66	2118.14	928.75	2550.73	1095.10
May	1709.16	1235.57	634.12	928.12	784.98
June	6673.35	1074.59	647.40	492.60	676.01
July	9174.14	1580.21	940.56	490.53	223.68
September	9228.55				
October	9372.29	1063.34	709.09	514.95	
November	2794.74	1686.27	1170.16	853.16	
December	2120.40	2259.71	500.77	729.70	
1928					
January	5287.23	3006.31	939.57	2272.22	1359.80
February	6278.33	3940.74	731.51	2258.30	2441.98
March	6271.34	4701.04	1088.65	3994.70	
April	5990.87	3098.62	730.93	1930.64	481.70
May	6844.25	913.10	744.72	779.80	191.86
June	7063.36	478.54	309.83	309.39	62.41
July	4748.25	733.57	567.60	287.33	
August	7109.39	829.20	633.33	267.61	66.70
September	4200.91	498.63	345.04	297.40	41.99

bright day. The intensities measured in the field on this date, and the Chicago Weather Bureau gram-calory data for the same hourly periods, are not exceeded by any other day on which a field trip was made, and this day is approached in brightness only by May 12, 1928 and June 15, 1928 between 12:00 and 4:00 P.M.

No selection was made in handling the data obtained and such unusual figures were to be expected. The average daylight intensities for any given period are quite generally within the limits observed by other workers for the same period.

Table II shows the hourly means for 1926 of the daylight intensities in the pioneer cottonwood associes. The complete data for all of the forest communities of the upland forest-on-sand sere of the Chicago Area have been compiled and are deposited in the University of Chicago Library (Park, 1929a).

To illustrate the normal seasonal cycle, with respect to the forest canopy, and the accompanying changes in daylight intensity, as received on the floor of the forest, a number of graphs have been constructed. In each case such

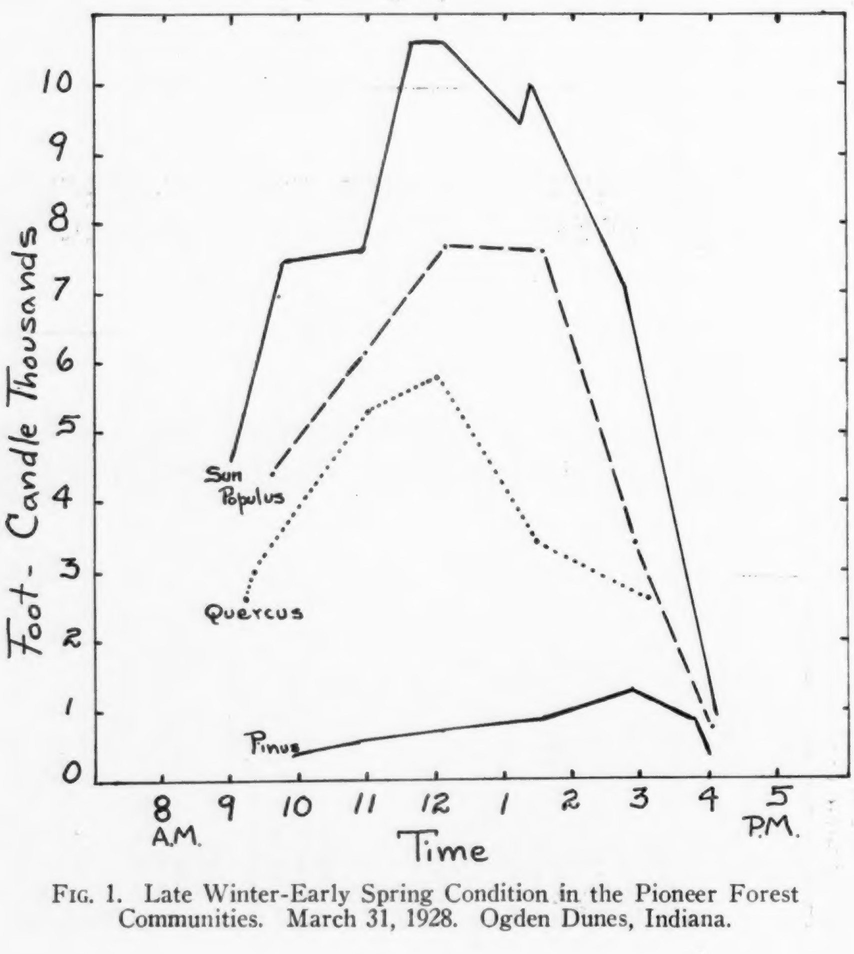

FIG. 1. Late Winter-Early Spring Condition in the Pioneer Forest Communities. March 31, 1928. Ogden Dunes, Indiana.

a graph is based on data taken in the field from a single field trip, and represents not only the general seasonal condition of the community concerned, but the exact conditions of daylight intensity existing in the community on the date given.

The condition indicated in Fig. 1 is that prevailing through the dune communities of the upland forest-on-sand sere in the late winter and early spring. At this time the deciduous associes, such as the black oak and cottonwood, are either bare of leaves, or are holding a remnant of last year's foliage, while the evergreen community, as the jack pine-cedar-bearberry, is preserving its normal amount of foliage throughout the winter months. Under these conditions the intensity of daylight is least on the conifer floor, and considerably more intense on the deciduous floors.

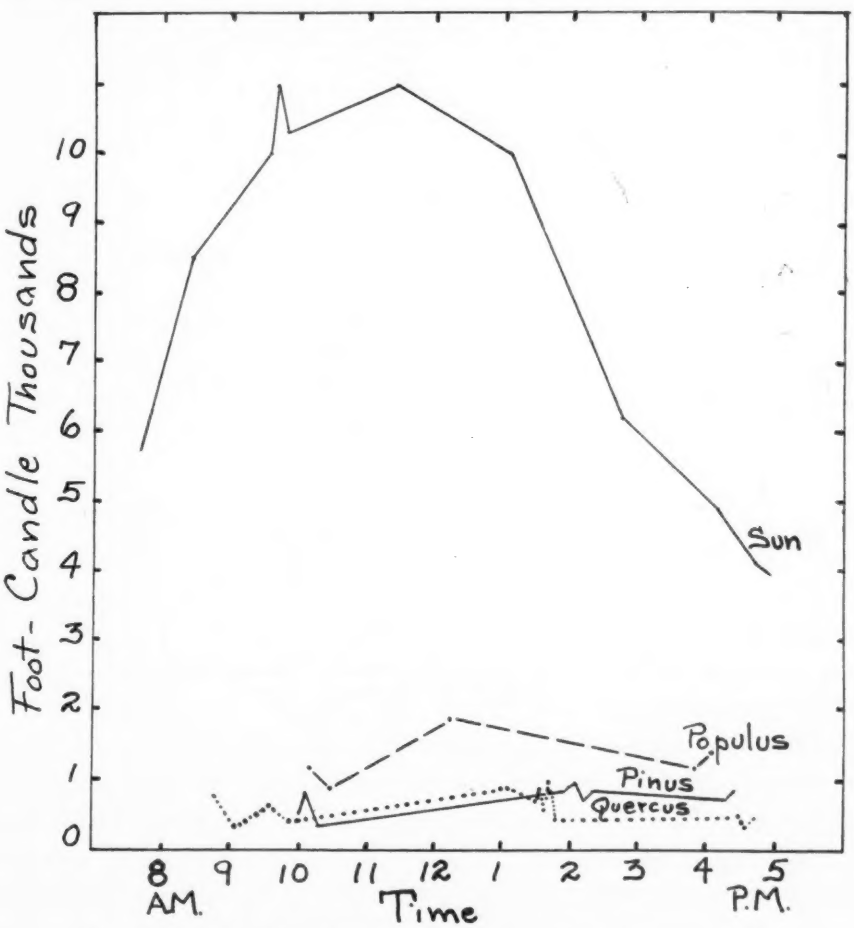

FIG. 2. Spring Condition in the Pioneer Forest Communities. May 29, 1928. Long Lake, Indiana.

In the middle and towards the end of the spring season (Fig. 2), the developing leaf buds, and first vernal foliage, tend to lower the daylight intensity penetrating to the floor of the deciduous communities. Under these

conditions the floor intensities in these latter are strikingly similar. Theoretically a time comes when the deciduous and evergreen communities are practically alike with respect to floor daylight intensity. Such a situation is approached in Figure 2, especially in the pine and oak associes. Note in this figure how the intensity lines fluctuate, depending upon the particular tree under which the daylight was measured.

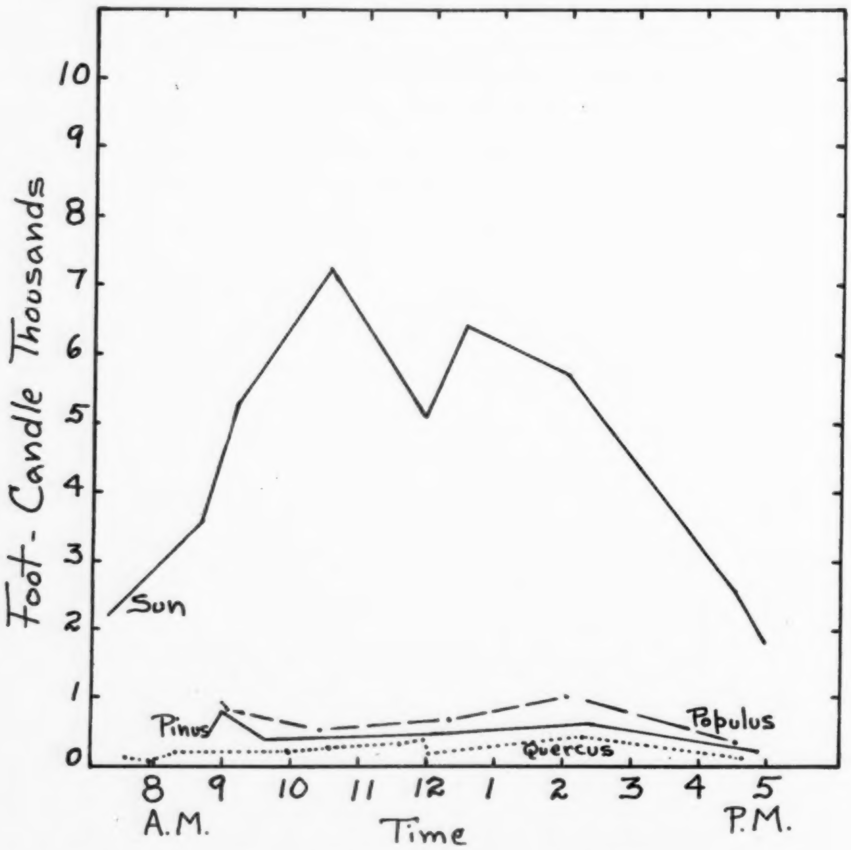

FIG. 3. Summer Condition in the Pioneer Forest Communities. July 29, 1928. Ogden Dunes, Indiana.

With the assumption of full foliage, the typical aestival condition is attained (Fig. 3). In this period the intensities of daylight on the forest floors are in perfect general accord with the position of these communities in seral succession as advanced by Cowles (1899, 1901), with the general position of each community with respect to the open beach and their respective beetle faunas (Park, 1930), and with the soil moisture and evaporation studies of Fuller (1911, 1912, 1912a). At this time the unobstructed sun is averaging generally from 7000 to 10,000 foot-candles, the pioneer cottonwood floor between 400 and 1500 or 2000 foot-candles, the pioneer conifer floor from 300 to 800 foot-candles, and the pioneer black oak floor from 100 to 400 foot-candles daylight intensity.

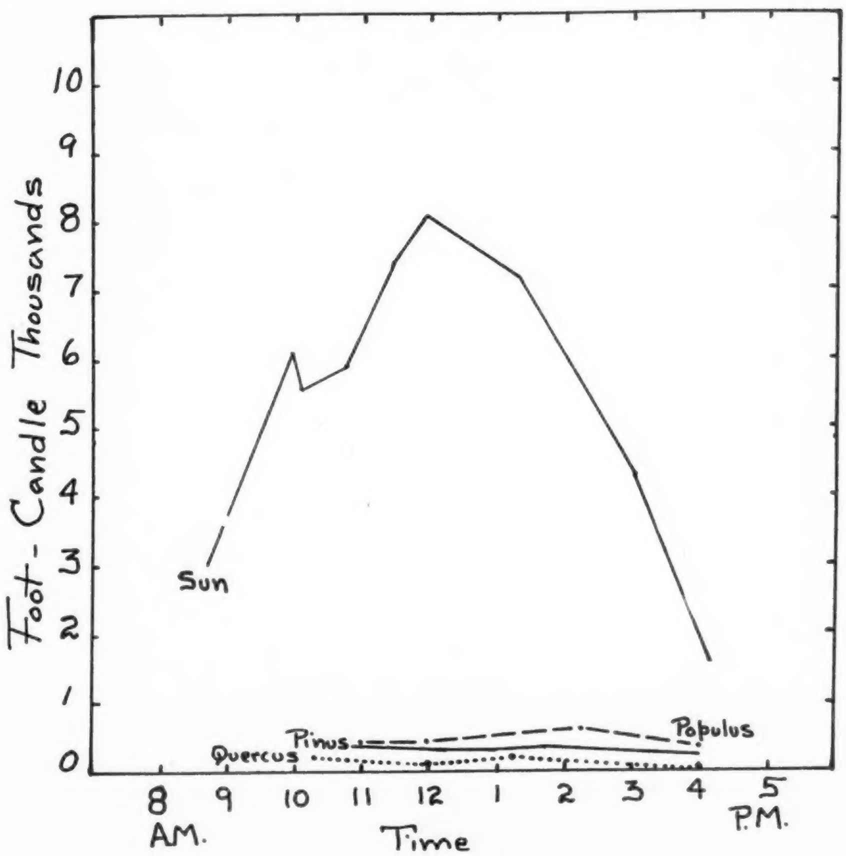

FIG. 4. Late Summer-Early Autumn Condition in the Pioneer Forest Communities. September 30, 1928. Ogden Dunes, Indiana.

The condition indicated in Fig. 4 persists through late summer, and into early autumn.

In the autumnal period (Fig. 5), the average daylight intensity remains high at first, and then slowly falls off. The intensity on the forest floor of the deciduous communities, however, begins to rise. This is due to the early fall of some part of the foliage. Such early decrease of canopy area is especially true of the cottonwoods which not only lose their leaves earlier than do the black oaks, but in general hold a more exposed position, with respect to Lake Michigan in the dune region of the Chicago Area, and consequently the dying foliage is more apt to be swept away by wind and sand blast action. This early loss of foliage, with accompanying increase of floor intensity, is counteracted in part, however, by the autumnal increase in opacity of the deciduous foliage. In the middle and late autumn a transition period, as noted in the late spring and early summer, is again reached. This would be expected since the deciduous communities tend to lose their foliage. The conditions prevailing in the conifer associes, however, are much more stable in this respect.

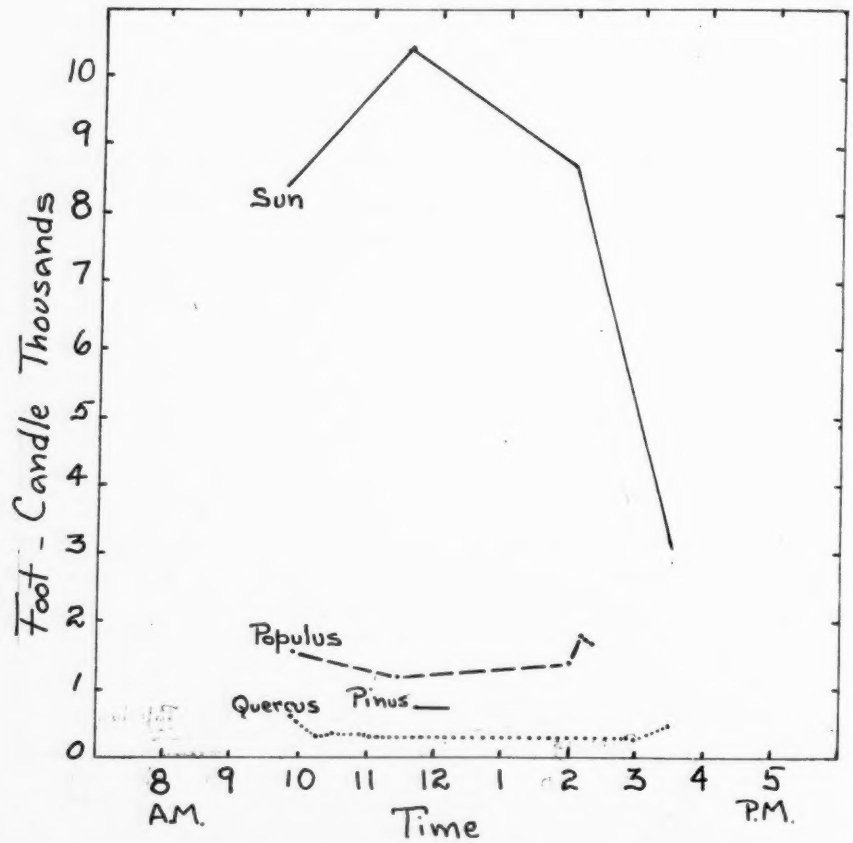

FIG. 5. Autumn Condition in the Pioneer Forest Communities.
October 27, 1928. Ogden Dunes, Indiana.

Finally the hibernal (hiemal) condition is reached again (Fig. 6), and the seasonal cycle may be said to be complete. At this time the deciduous communities have a higher average floor intensity of daylight than the evergreen communities. It should also be noted that the daylight intensity on the evergreen floor tends to be lowered also by a packing of snow and ice on the thickly set needles. This serves to reflect and absorb some daylight which might otherwise have penetrated to the floor.

The daylight intensity of the sunflecks on the deciduous floors roughly parallels the intensity of the unobstructed sun through the year. The area covered by sunflecks tends to diminish through the vernal period, being at a minimum in the estival (aestival) period. At this time the sunfleck intensity, however, is usually at a maximum. Similarly, the sunfleck area tends to increase and the intensity of daylight to decrease through the autumnal, and into the hibernal season. In the latter period the sunfleck area is usually at a maximum. In Fig. 6 the effect of a large sunfleck on the floor is shown for the black oak community on the morning of January 31, 1928. The intensity of this fleck is seen to be very much greater than the floor intensity.

Such sunfleck readings, however, were not averaged into the floor daylight intensity means, *per se,* and are treated later in the report.

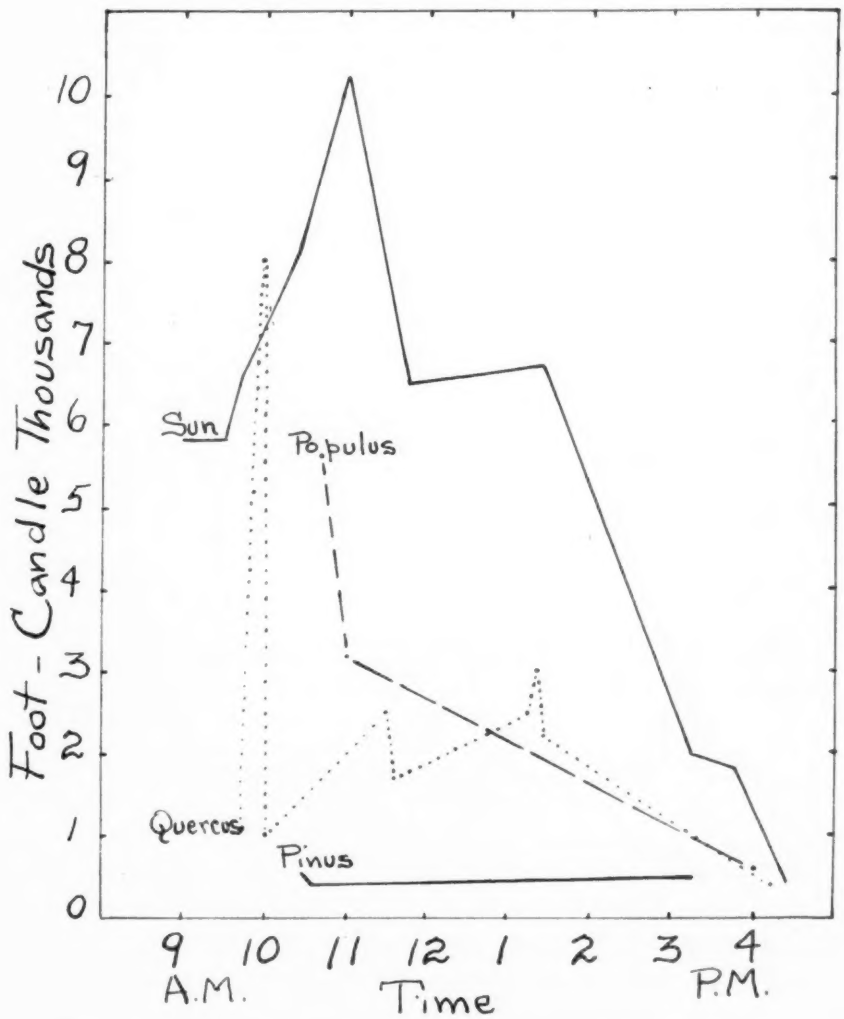

FIG. 6. Winter Conditions in the Pioneer Forest Communities. January 31, 1928. Ogden Dunes, Indiana.

The winter condition in the climax association (Fig. 7), is the same in general as that of the other deciduous communities at this period, especially with respect to daylight intensity as measured here. The average intensity penetrating to the floor, however, may be somewhat lower than that of the pioneer deciduous associes, since there is frequently a greater amount of branch and twig interference in the former.

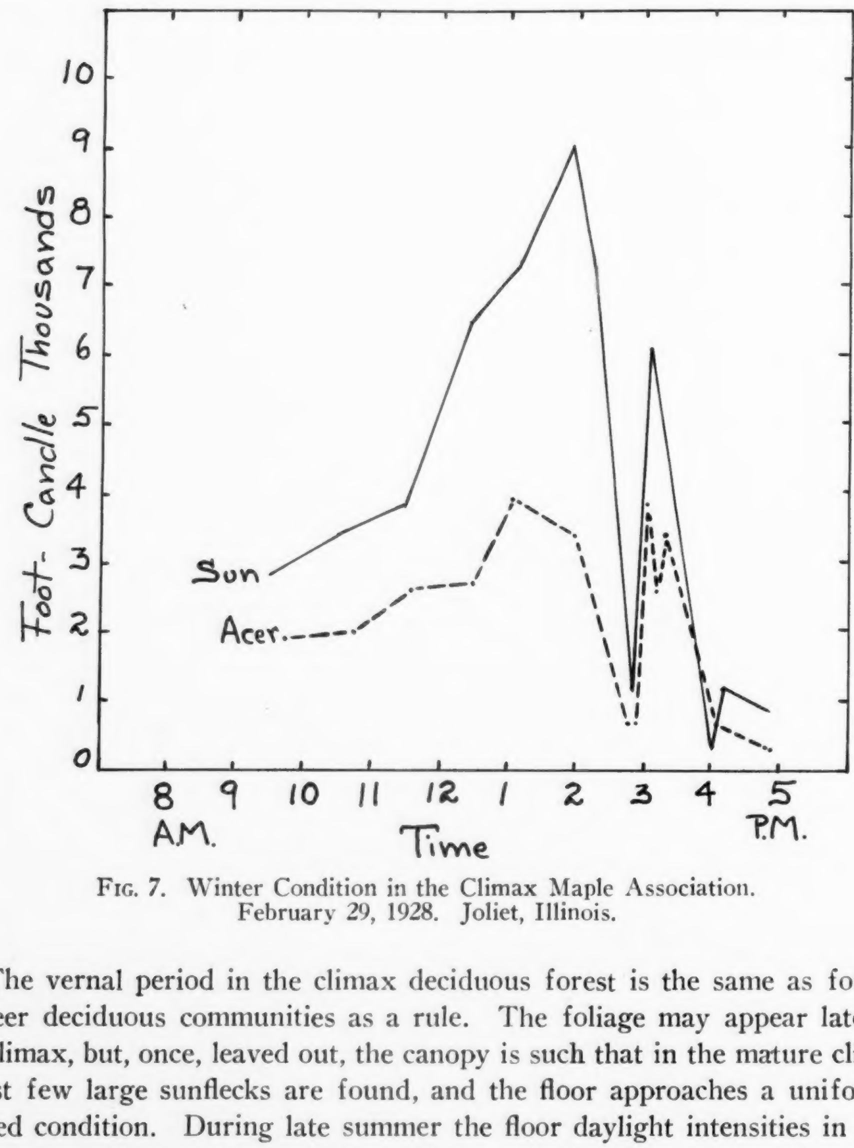

FIG. 7. Winter Condition in the Climax Maple Association.
February 29, 1928. Joliet, Illinois.

The vernal period in the climax deciduous forest is the same as for the pioneer deciduous communities as a rule. The foliage may appear later in the climax, but, once, leaved out, the canopy is such that in the mature climax forest few large sunflecks are found, and the floor approaches a uniformly shaded condition. During late summer the floor daylight intensities in such a climax usually fall between 50 to 150 foot-candles, but may run below 25 foot-candles in certain parts of the forest. Figures 8 and 9 show, in a general way, the daylight intensity conditions for the aestival and autumnal periods in the climax forest respectively.

The seasonal variation in the intensity of daylight, with respect to the communities of the upland forest-on-sand sere, is presented in Fig. 10. This graph is based on the summation of the hourly means (Table III), and shows on the same scale the daylight intensity in foot-candles of the unobstructed sun, and the floor intensities in the pioneer cottonwood, pioneer conifer, pioneer black oak, and climax maple communities. It represents a nearly

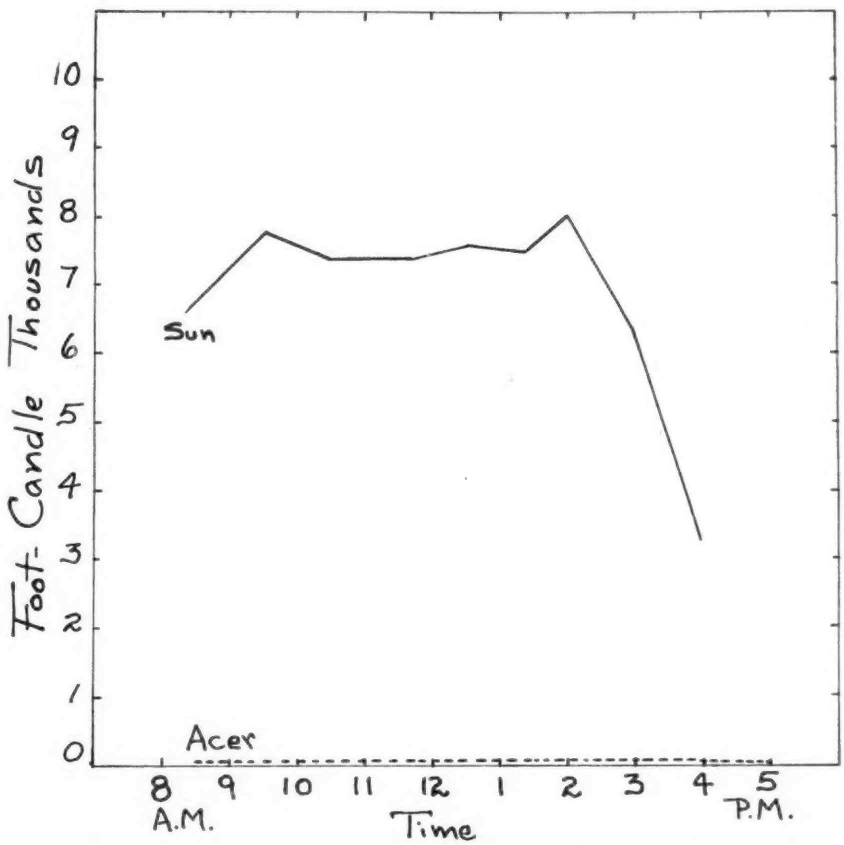

FIG. 8. Summer Condition in the Climax Maple Association. June 14, 1928. Joliet, Illinois.

continuous record, based on observations in the field from eight in the morning until four in the afternoon, for eighty-one months. In general it will be seen that the cyclic character of the curves for each community is duplicated each successive year. This indicates that there is correlation between daylight intensity penetrating to the floor of a forest, and the seral position and seasonal aspect of the community in the upland forest-on-sand sere of the Chicago Area.

4. CHECK OF THE DATA BY PYRHELIOMETRIC MEASUREMENTS

A check of the foot-candle intensity data was made by comparing the intensity curve of the unobstructed sun, as measured in the field, with a curve obtained from a tabulation of the hourly means for the same days in gram-calories per square centimeter of horizontal surface. Data for the latter were obtained from the University of Chicago Observatory and from the Chicago Weather Bureau, through the courtesy of Mr. P. E. Johnson and of Mr. Whitney respectively. They were based on solar and sky radiation figures from electrically recording thermopiles, known as Weather Bu-

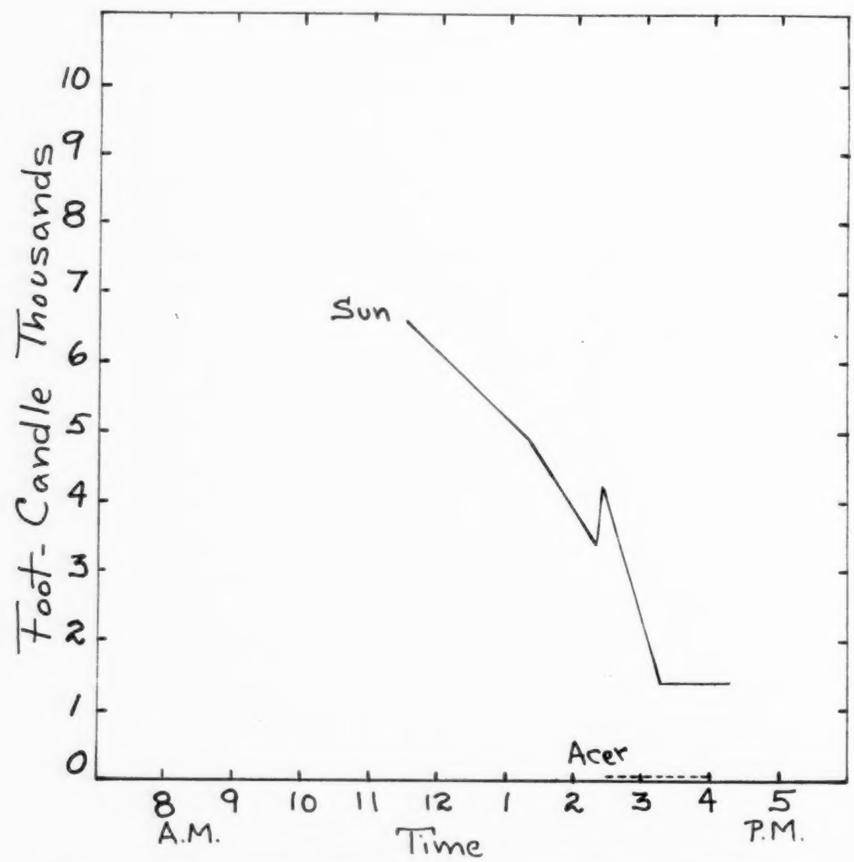

FIG. 9. Late Summer-Early Autumn Condition in the Climax Maple Association. September 29, 1928. Joliet, Illinois.

reau Thermoelectric Recording Pyrheliometers. Such instruments belong in the category of light-measuring apparatus known as "Radiometric Instruments," and are widely used by weather recording stations. A great deal of data has been assembled upon light in general, and radiometry in particular. The following citations largely cover the field, either by discussion or by the inclusion of valuable bibliographies: Angström and Dorno (1921), Bates and Zon (1922), Chapman (1926, pp. 6-7; 15-27), Coblentz (1913, 1919, 1921), Dorno (1922), Kimball and Hobbs (1923), Klugh (1925), Pulling (1919), and Shelford (1929, pp. 309-336; 445-464).

Figures from radiometric observations were chosen especially because (1) the data are trustworthy, (2) they are compiled from an entirely different source by different workers, (3) although measuring the intensity of daylight the figures represent an entirely separate effect than that expressed by foot-candles, hence they are especially commendable as a check, and (4) Kimball (1924) used such data for his comparisons.

The pyrheliometric data referred to were taken from records covering the period between 8:00 A.M. and 5:00 P.M. on the days spent in the field

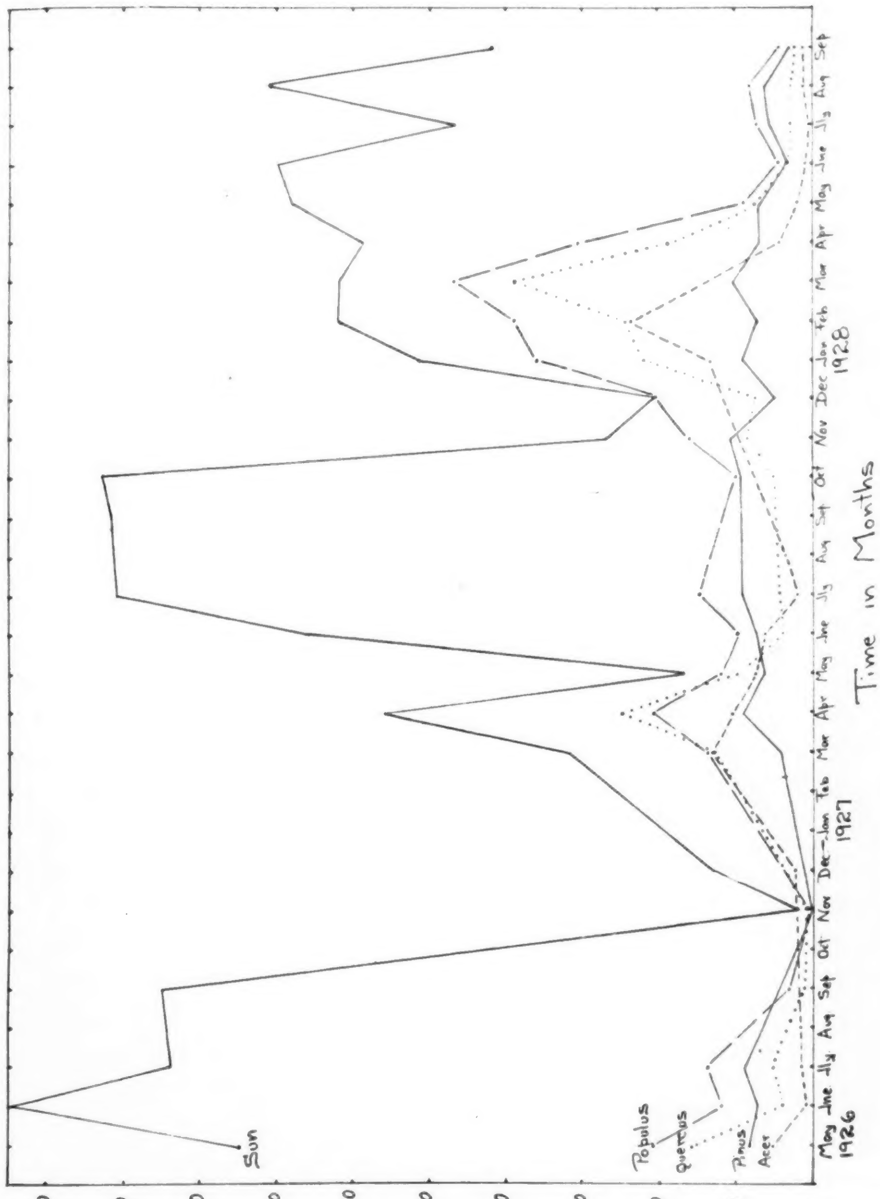

FIG. 10. Seasonal and Seral Distribution of Daylight Intensity in the Upland Forest-on-sand Sere of the Chicago Area. Based on hourly mean averages, and corrected to Central Standard Time.

(see Table I for comparable foot-candle data), and the monthly averages in gram-calories per square centimeter of surface were compiled for the same periods over which the intensity of the unobstructed sun was measured in foot-candles by the Macbeth Illuminometer (Table IV).

TABLE IV. *Summary of Daylight Intensity in the Chicago Area, Given in Gram-Calories.*

The following figures are averages, per month, for the period from May, 1926 to September, 1928, in gram-calories per square centimeter of horizontal surface. For comparative data see the averages for the unobstructed sun in foot-candles (Table III).

Month	*1926*	*1927*	*1928*
January			13.7
February			22.9
March		26.6	36.6
April		33.3	32.6
May	25.7	18.5	43.6
June	41.4	38.3	52.7
July	37.7	42.6	41.2
August	...	...	40.9
September	42.8	36.5	29.2
October	...	24.3	...
November	7.7	6.6	...
December	8.8	10.2	...

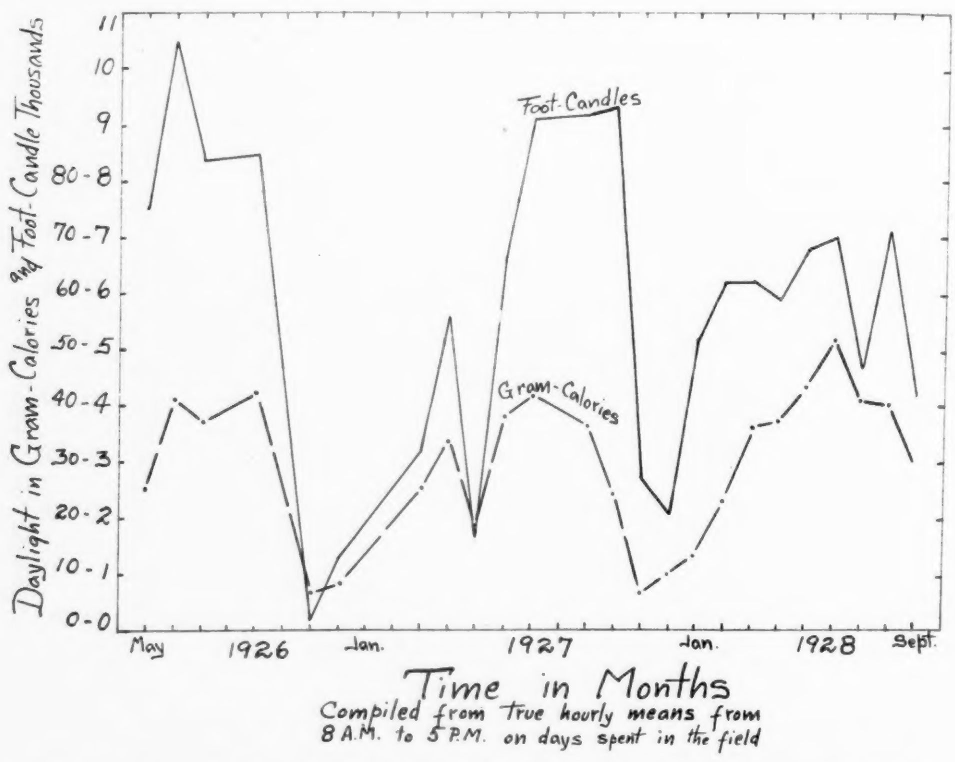

FIG. 11. Seasonal Distribution of Daylight in the Chicago Area in Foot-candles and Gram-Calories. (Curves based on data in Tables III and IV).

In Figure 11 the data in Tables III and IV for the daylight intensity of the unobstructed sun have been plotted. The lower curve represents the daylight intensity in gram-calories, the upper curve shows the intensity in foot-candles.

On examination of these two curves a remarkable close correlation between their loci is apparent; remarkable when one remembers that the data for each curve was obtained with different instruments and different ob-

servers. Each curve represents a different phase of daylight expressed in different units of measurement. Again, whereas the foot-candelage was taken in the field (from 30 to 50 miles from Chicago), the gram-calory figures were taken in Chicago, and hence the incident daylight was subjected to any absorption and scattering effects as a consequence of the smoke pall. Despite this difference in geographic location, and the possible differences in atmospheric condition, the curves support one another. Thus the sudden drop in intensity in May, 1927, between two high points on either side (April and June) was originally thought to be due to an irregularity in the illuminometer, or in faulty collecting of data. However, some ten months later the gram-calory curve was plotted and the same drop was found, indicating that the data were sound, but that the days that were spent in the field in May, 1927, were unusually overcast.

The writer understands that this check does not apply directly to the intensity curves in foot-candles for the various forest communities studied, but applies directly only to the intensity curve for the unobstructed sun. However, the check on the floor intensities of the forest communities is indirectly shown by the very nature of the factor measured, and by the close correlation through eighty-one months between the unobstructed sun intensity curve and any given forest community curve. A direct check on the forest community intensities might be obtained by the use of a portable pyrheliometer. Where such an instrument could be taken into the field and the daylight penetrating to the forest floor measured *in situ*, in both foot-candles with a Macbeth Illuminometer, and in gram-calories with a portable pyrheliometer, such a check would be of great corroborative value. A semi-portable Richard pyrheliometer, as noted by Klugh (1927), might be used to advantage here, and a comparative check could be obtained by measuring ultraviolet radiation and foot-candle intensity. Portable ultraviolet photometers have been only recently developed (Klugh, 1930), however, and open the way to a more complete knowledge of light conditions in the forest community.

5. THE RELATIVE AMOUNT OF SHADE AND SUN IN A GIVEN AREA

In order to obtain a close approximation of the illumination complex in a given associes one must know the proportion of the area covered by the associes which is shaded as well as the illumination intensity in the unshaded and shaded areas. Actual inspection of the forest associes such as were studied for the present report shows that in the pioneer associes much of the ground surface is exposed to the full sunlight intensity (or nearly so), while other parts of the forest floor are more or less completely covered by crown shade. The amount actually shaded then is dependent upon at least two factors, the density of the stand and the density of the crown shade. A consideration of the former will be deferred for a few pages.

SUN-FLECKS

The area covered by crown shade may be entirely shaded to approximately a uniform degree but more usually there are flecks of light ranging from bright sun-flecks to regions only slightly less densely shaded than are the surrounding areas of least illumination intensity. Not only does the daylight intensity of the sun-fleck change with the time of day, and time of year, but obviously varies with the nature and extent of the forest canopy. The practical question which arises concerns itself with how much of the forest floor is receiving the different light intensities or more pointedly, within the area covered by the crown shade, what is the proportion of sun-flecks to shaded areas? The answer to this question must be quantitative and should be applicable to other forest studies in order to be at all satisfactory. A partially subjective method was used to answer this question as far as possible, viz. one that would indicate the amount of floor shaded and sun-flecked. This has been termed the "Percentage of Shade Method."

"One hundred forty pound egg-shell paper" was obtained from the University of Chicago Press, the sheets being 50 by 38 inches with an area of 1900 square inches. The average weight of one of these sheets was found to be 130.00 grams (dry weight). If such a sheet was exposed to a uniformly shaded area, e.g. if no sun-flecks appeared outlined on its surface, the sheet was said to be entirely shaded and the percentage of shade 100%. Conversely, when laid in the open sun the shaded areas were absent, and the percentage of shade was zero. On this assumption, then, 130 grams = 100% shade, and the percentage of shade of any given sheet of paper (e.g. any 1900 square inches of forest floor surface) could be obtained by exposing the sheet, drawing in with soft graphite pencil the outlines of the sun-flecks as accurately as possible, bringing the sheet back to the laboratory and, after drying to drive off moisture, cutting out the portions illuminated. In this way the shaded areas were left and these were weighed to an accuracy of $\pm$ 2.5 grams, and the percentage of shade calculated.

It should be observed that there was a tendency for the deeper and lighter shaded areas to cancel and so give an average amount of shaded area. The approximate outlines of the actual sun-flecks were drawn in on the paper and the differences in shade intensities were disregarded in this report. Further, since the sun-flecks were constantly shifting, there was a continually changing density of shade. It should be further noted that the percentage of sun-flecks varies markedly at different hours of the day, hence the percentage of shade from such areas can be only actually shown for a given moment. The mean of many such readings, however, gives a fair approximation of the usual amount of shaded and sun-flecked areas under the trees of the different forest communities.

Sheets of paper were taken afield for nine months, and a number of sheets were used for each community on each trip in order to allow the law

TABLE V. *The Percentage of Shade*

ASSOCIES 1928	TIME (Central Standard)	INTENSITY (Foot-Candles)	PERCENTAGE OF SHADE (In per cent)
JANUARY 5			
Cottonwood	1:36 P. M.	2522.47 to	18.60
(Populus deltoides)		2690.64	
Conifer (Pinus banksiana)	12:00	1580.75 to	91.40
		1681.65	
	1:58 P. M.	1278.05 to	100.00
		1311.68	
Oak (Quercus velutina)	11:40 A. M.	2017.98 to	23.90
		2102.06	
JANUARY 10			
Climax Maple	11.55 A. M.	1597.56 to	21.5
(Acer saccharum)		1849.81	27.6
	12:40 P. M.	2858.80	21.9
	12:42	2186.14	20.1
	1:55	588.57	30.0
			31.1
	2:20	975.35	21.5
	2:30	1109.88	27.6
JANUARY 31			
Cottonwood	10:40 A. M.	4909.41 to	20.11
		6403.59	15.15
			15.15
Conifer	10:30	521.31 to	88.46
		554.94	95.00
			83.26
			91.30
			100.00
Oak	9:45	2134.53 to	22.33
		2774.88	
	9:44	924.90 to	20.11
		1008.99	
	11:35	2522.47	15.15
		3363.30	17.00
			15.15
	(holding last year's foliage)		43.00
			17.00
FEBRUARY 28			
Cottonwood	9:53 A. M.	3842.15	10.57
		5336.32	16.30
	10:47	6617.04	
		7043.94	
Conifer	10:15	554.94–571.76	83.61
	10:15	790.37 to	95.07
	10:41	807.19	100.00
Oak	9:10	2354.31	27.71
	9:12	2522.47	14.38

TABLE V. *(Continued)*

ASSOCIES 1928	TIME (Central Standard)	INTENSITY (Foot-Candles)	PERCENTAGE OF SHADE (In per cent)
FEBRUARY 29			
Maple	2:00 P. M. 2:07	3372.55 to 4269.06	14.38 26.30 24.07 26.30
MARCH 24			
Cottonwood	9:33 A. M.	6617.04	26.30
Conifer	10:00 A. M.	2186.14 to 2354.31	84.40
Oak	9:13 A. M. 9:20 12:47 P. M.	2134.53 to 2774.88 4055.60 4204.12 (trunk shade)	44.20 31.60 8.72
MARCH 31			
Cottonwood	9:40 A. M.	4269.06 to 4482.51	22.07 16.34
Conifer	9:50	336.33	87.40
Oak	9:21	2858.80 to 3026.97	18.20 18.20 16.34
APRIL 26			
Cottonwood	10:35 A. M. 10:36	5982.06	25.96 10.57
Conifer	10:30 A. M. 10:50	1649.49 to 673.26	100.00 85.00
Oak	10:15 A. M. 10:16	218.81	16.34 18.26
MAY 22			
Cottonwood	9:00 A. M. 2:05 P. M.	791.08 1430.68 to 942.56	 54.70
Conifer	9:25 A. M.	706.92	87.40
Oak	8:40 2:20 P. M.	807.91 1009.89 to 1043.55	 57.60
MAY 23			
Climax Maple	9:00 A.M.to 9:20	420.79	 88.55
JUNE 14			
Climax Maple	10:30 A. M.	52.35	89.84 to 100.00

TABLE V. *(Continued)*

ASSOCIES 1928	TIME (Central Standard)	INTENSITY (Foot-Candles)	PERCENTAGE OF SHADE (In per cent)
JUNE 15			
Cottonwood	9:45 A. M.	265.93 to 589.10	58.65
Conifer	12:15 P. M.	336.63–353.46	85.57
Oak	9:00 A. M.	193.56 to 218.81	81.92
JULY 29			
Cottonwood	9:00 A. M.	841.58	77.88 88.53
Conifer	8:45 A. M.	521.77 to 538.61	95.19
Oak	7:30 A. M.	168.31 to 185.14	72.80 79.80 91.34
AUGUST 7			
Cottonwood	9:15 A. M.	622.76 to 538.61	85.53
Conifer	9:00 A. M.	673.26	87.50
Oak	8:40 A. M.	157.05 to 168.31	87.50 77.34 70.19
AUGUST 10			
Climax Maple	9:00 A.M. to 10:10 A. M.	59.33	87.50 99.03 95.15 95.15 95.15 100.00 89.42
AUGUST 14			
Cottonwood	1:06 P. M.	1009.89 (marginal)	39.42
Conifer	12:56 P. M. 1:03	471.28 908.90	72.11 52.88
Oak	12:30 P. M.	841.58	70.19 62.50
	12:43	311.38	62.50 lost.
AUGUST 31			
Cottonwood	1:20 P. M.	1178.21	68.26 79.80
Conifer	12:50 P. M.	757.42 841.58	91.34 72.11
Oak	12:15 P. M.	286.13	75.96 89.42 75.90

TABLE V. *(Continued)*

ASSOCIES 1928	TIME (Central Standard)	INTENSITY (Foot-Candles)	PERCENTAGE OF SHADE (In per cent)
SEPTEMBER 23			
Oak	11:30 A. M.	387.12	72.11
SEPTEMBER 29			
Climax Maple	2:30 P. M.	59.33	85.53
			95.15
			93.20
			85.53
SEPTEMBER 30			
Cottonwood	11:00 A. M.	572.27	66.30
		420.79	68.26
Conifer	10:50 A. M.	462.86	83.60
	10:53	471.28	85.53
Oak	10:21 A. M.	208.71	81.70

of averages to operate. To obviate the subjective element as much as possible, a number of people have selected the area to be worked, drawn in the sun-flecks, cut these out in the laboratory, and weighed the resulting shaded portions from time to time, so that the data presented are not the work of one individual. Despite care with such details, the writer feels that the method is still unsatisfactory, but even so, the Percentage of Shade method has answered some interesting questions, and brought others to notice, especially the rôle of sun-flecks in determining the distribution and behavior of forest animals.

The data on percentage of shade under the tree crowns are given at length in Table V, and represent readings up to October, 1928. Since each reading represents a fairly fleeting condition, it has been thought advisable to present more complete data than is needed to make the illumination readings of light intensities convincing.

TABLE VI. *Summary of the Percentage of Shade.*

The mean average percentages of shade for the four forest communities studied from January to October, 1928 are presented in the following table; the readings being taken usually between 9 A. M. and 2 P. M.

Month	*Cottonwood*	*Conifer*	*Black Oak*	*Sugar Maple*
January	17.70	94.30	22.60	26.20
February	13.40	92.80	21.00	22.70
March	26.30	84.40	34.50	....
April	18.20	92.50	17.30	....
May	54.70	87.40	57.60	88.50
June	58.60	85.50	81.90	90.00
July	83.20	95.10	81.30	....
August	77.80	80.70	79.40	95.20
September	67.28	84.56	76.90	87.35

The graph in Figure 12 is based on the averages in Table VI. It illustrates the seasonal cycle in the upland forest-on-sand sere with respect to the amount of shade per unit of floor, in terms of the percentage of shade. Unfortunately the data for the climax maple association is not complete, data on percentage of shade not being compiled for March, April and July. However, it will be seen that the general character of the curve for this community follows the other complete curves of the deciduous communities. In this graph it is interesting to observe how relatively constant the evergreen curve is in contrast to the curves for the deciduous communities. This is to be expected, however, since the percentage of shade follows a seasonal rhythm which is largely dependent upon the thickness and character of the canopy.

6. Density of Stand

Another factor which determines the amount of forest floor shaded concerns itself with the density of the forest stand, or, in other words, the closeness of the trees of a given community. It is common knowledge that in a uniform stand, largely dominated by one or several ecologically equivalent species, trees tend to be spaced at an average, uniform distance from each other. This is the natural result of competition for soil, moisture, light, and other limiting factors. Such a situation was found in the representative communities in the upland forest-on-sand sere of the Chicago Area. In Table VII data on the density of stand, especially those phases concerned in this report with the relation of stand density to forest illumination problems, are given as averages for the forest communities studied.

TABLE VII. *Comparative Data on Density of Stand.*
Unit area used was a square of forest floor, 50 by 50 feet (A).

Associes	*Average number of trees per unit area*	*Average diameter of crown in feet*	*Average area in crown shade (πr^2) in sq. ft.*	*Average sq. ft. of unit area in shade (A-P)*	*Average sq. ft. of unit area in sun. (P)*
Cottonwood	4.0	11.28	99.90	399.60	2100.40
Conifer	10.5	8.28	53.81	565.00	1935.00
Black Oak	16.4	11.20	98.52	1615.72	884.28
Climax Maple	10.3	19.87	310.08	3100.80*	0.00

In a uniform stand, such as a climax sugar maple forest, the trees have in general attained an average height, diameter, and distance apart due to competition. Under such conditions the foliage of a single tree will average about the same as that of its neighbors. This is true for the trees away from the forest margin. Given the same amount of foliage and the same time of day, the amount of shade per unit of floor in one portion of the forest should approximate a similar unit of another portion. Hence by random sampling

* A-P is more than the unit area taken (2500 sq. ft.), due to overlapping of crowns.

over various sections of the forest (or by the transect method), the percentage of shade for the community as a whole may be obtained.

If the average amount of shade per unit of floor for a community is known, as well as the daylight intensity penetrating to the floor, and the average distance apart of the trees in a stand, one has the key to an understanding of the distribution of the herbaceous stratum and the distribution of the fauna of the forest floor, since the presence or absence of light, and its intensity, are known to have a marked influence on the distribution of many species. If the intensity of the light penetrating to the floor, and the amount of this light per unit of floor be known, the possibilities for interpreting distribution become still more probable if other regulatory factors, such as temperature, humidity, and wind, are also considered. This is the more probable since light intensity is known to operate so as to influence an animal in the selection of its habitat niche, not only on account of brightness, but also because of resulting temperatures induced by the substrate of leaves

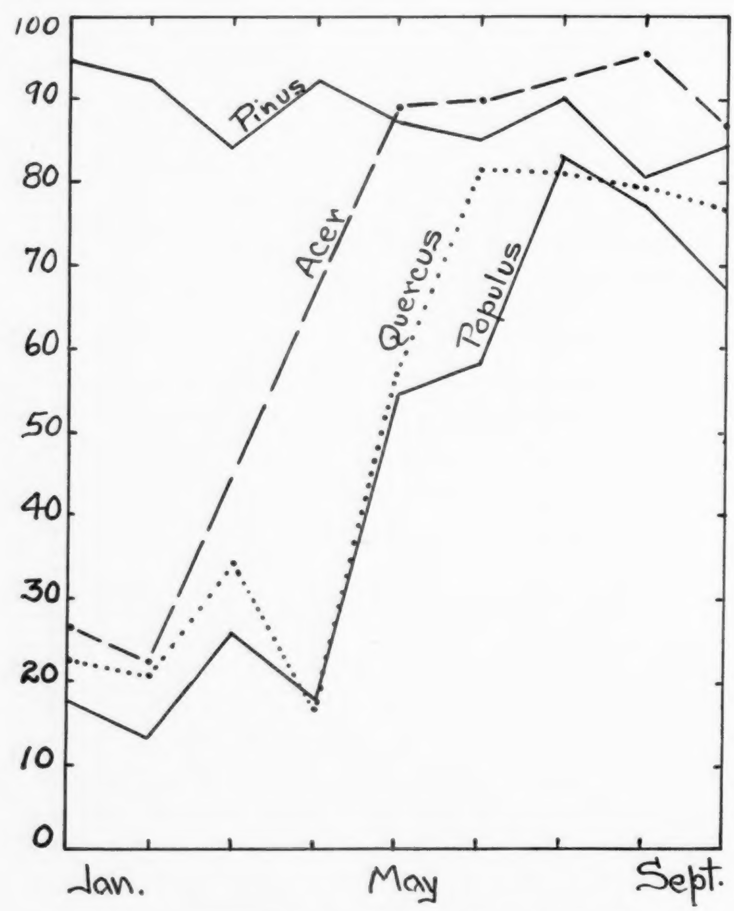

FIG. 12. Percentage of Shade for the Upland Forest-on-sand Sere of the Chicago Area. January to September, 1928. Based on data in Table VI.

and debris absorbing and radiating energy in the form of heat, which in turn affects relative humidity. Closeness of stand and the density of foliage also affect wind velocity, which in turn affects temperature and humidity independently of the effects of light, as has been shown in part by Allee (1926) working in the tropical rain forest of Panama.

The data in Table VI show that the relative amounts of shaded floor, as measured by the shade percentage of the crowns, and not by the density of stand, are comparable to the general seasonal cycle for a given forest community. As would be expected, it is found that following the vernal appearance of foliage in the deciduous communities, the percentage of shade increases, reaches a height in summer and falls off in autumn when the leaves begin to be shed. Such a sequence of events, proceeds differentially in different associes, and is also related to the seasonal increase and decrease in the intensity of daylight. The coniferous community, as represented by the pioneer jack pine *(Pinus banksiana)—Juniperus-Arctostaphylos* complex, is largely independent of the seasonal cycle, and preserves throughout the year a more or less even amount of shade which on the average is much denser than that found in the deciduous communities. This percentage of crown shade is equaled or surpassed by the more mesophytic deciduous communities when the latter are in full foliage, and similar relations are shown by the studies on light intensity.

It is to be noted that the uneven character of the percentage of crown shade curves (Fig. 12), as well as of those for intensity (Figs. 1-9) in a lesser degree, are due to an inability to obtain enough readings close together over a long period of time, as would be obtained by a recording instrument. This is an insufficiency of data which it is hoped time will remedy.

7. Ecological Light Units

In the preceding pages records have been given of the intensity of daylight of the unobstructed sun and of that penetrating to the floor of certain forest communities as measured with a Macbeth Illuminometer. The amount of shade over a given area of forest floor has been calculated in terms of percentage of shade.

With respect to the ecological significance of these data, an attempt was made to bring together all the factors concerned with: (1) the daylight intensity of the unobstructed sun, (2) the daylight intensity of the forest floor in the shaded and in the sun-flecked areas, (3) the amount of floor shaded and sun-flecked, and (4) the density of the forest stand, into one formula in which the resultant would be an expression of these factors for a given unit area. Such an expression has been called the Ecological Light Unit for that area.

Let A=a unit area (2500 square feet).

A—P=the shaded portion of the floor of this unit area.

P=the sunlit portion of the same area (e.g., the natural clearings and open spaces).

S=the percentage of the shaded area covered by sun-flecks.

1—S=the percentage of the shaded area actually in complete shade, i.e., not in sun-flecks.

q=the intensity of daylight in the completely shaded regions, i.e. (1—S).

q'=the intensity of daylight in the sun-flecks, i.e. (S).

Q=the intensity of daylight from the unobstructed sun in the open parts of the unit area, i.e. (P).

Then the following formulation can be stated:

$$\frac{PQ+(A-P)\ (Sq'+(1-Sq))}{AQ}=\text{Ecological Light Unit (E.L.U.)}$$

Where A—P is more than the unit area taken, due to the overlapping of crowns, as in the climax associations, P=O, and the above formula can be used for this special condition in the following form:

$$\frac{OQ=(A-O)\ (Sq'+(1-Sq))}{AQ}=\text{E.L.U. for the mature climax forest.}$$

To obtain the value of q', or the daylight intensity of the sun-flecks, a series of readings were made on portions of the forest floor. The following values were found to approximately represent the q' for the various communities throughout the upland forest-on-sand sere of the Chicago Area in the summer of 1929. These values were further checked by random q' readings during 1926 and 1927, but since q' was not specifically determined throughout the year, the value of q' should be considered as a more or less empirical one at present. A sample of the data for the climax sugar maple association is shown in Table VIII. From this the ratio of q'/Q was developed.

TABLE VIII. *The Value of q' for the Climax Sugar Maple Floor for Eight Days Between July 2 and 31, 1929.*

Time	*Unobstructed Sun in Foot-Candles (Q)*	*Sun-Flecks in Foot-Candles (q')*	*Ratio of q'/Q*
9:30 A.M.	5661.60	740.59	.131
10:30 A.M.	5127.48	740.59	.144
11:30 A.M.	12925.48	8196.88	.633
12:00 Noon	12605.07	8322.43	.666
12:30 P.M.	13246.00	1627.05	.118
1:00 P.M.	11773.22	6119.07	.526
1:30 P.M.	9542.82	1941.24	.203
2:30 P.M.	9878.54	1999.78	.202
3:30 P.M.	9507.21	4484.87	.472
4:00 P.M.	6380.14	3465.08	.544
4:30 P.M.	6623.00	1178.21	.145
		Average:	.346Q = q'

The average intensity for the unobstructed sun in Table VIII is 9388.23 foot-candles, and 3528.71 in the sun-flecks, giving the value of .376 for the ratio of the average. From this kind of data the following tentative values were assigned to q':

q'=Q in January, February, March and April (before foliation) for the pioneer deciduous communities (Cottonwood and Black Oak), and the climax Sugar Maple associations.
q'=.5Q in May, June, July, August and September (foliation), for the pioneer deciduous communities (Cottonwood and Black Oak).
q'=.5Q for the pioneer Conifer community.
q'=.333Q for the climax associations for May, June, July, August and September.

On this basis the E. L. U.'s for the upland forest-on-sand sere of the Chicago Area were calculated from the data available. These are given in Table IX.

TABLE IX. *Ecological Light Units for the Upland Forest-on-sand Sere of the Chicago Area, for January to September, 1928.*

(Compiled from Tables III, VI, and VII)

Month	*Cottonwood*	*Conifer*	*Black Oak*	*Climax Maple*
January	.988	.818	.917	.805
February	.986	.806	.913	.862
March	.989	.859	.919	...
April	.986	.808	.924	...
May	.888	.810	.533	.063
June	.880	.799	.435	.041
July	.874	.805	.446	...
August	.872	.812	.439	.025
September	.879	.807	.464	.051

The figures in Table IX represent the E. L. U.'s for the floor only, and are complete only as averages for 1928. As a consequence of insufficient data on the percentage of shade for the climax sugar maple forest in March, April, and July, no E. L. U.'s were calculated for these three months. Figure 13 shows the seasonal variations in the ecological light units for the forest communities studied, and brings out the difference in range of the ecological light units for each community.

It should be noted that comparison of these light units for any community with those of another community should take into account the factor of time of day and time of year where possible. It is believed that this method has ecological value since it brings a number of factors together into a workable unit, and makes a quantitative estimate of illumination possible on the basis of several aspects of the light present.

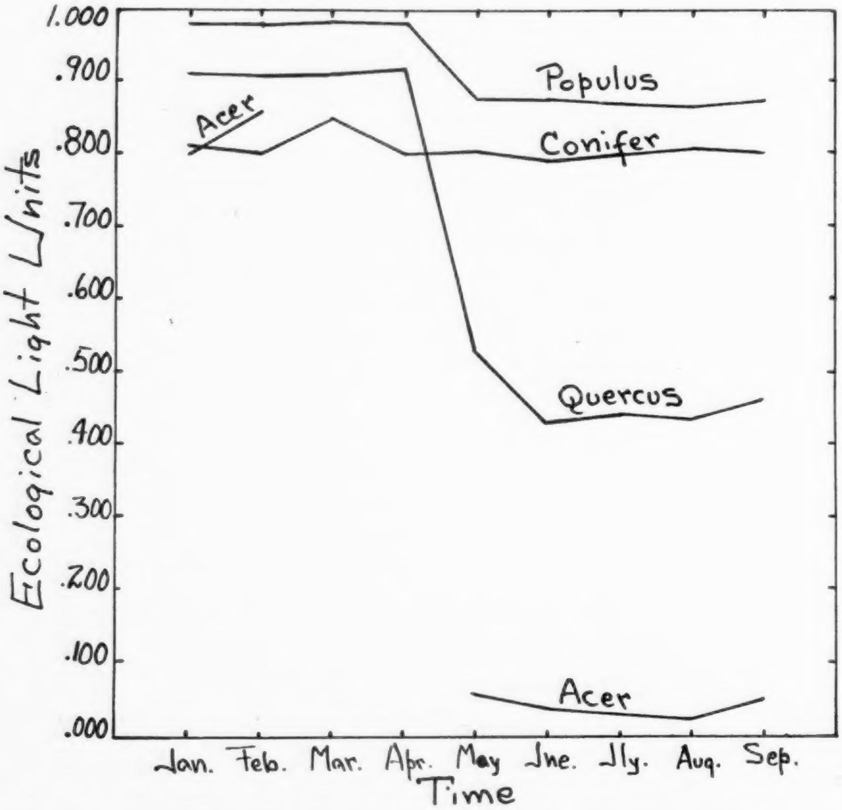

FIG. 13. Ecological Light Units for the Upland Forest-on-sand Sere of the Chicago Area. (January to September, 1928). Based on Table IX.

8. DISCUSSION

The original formula, constructed for the purpose of determining the Ecological Light Unit for a given community at a given time, is complex, being composed of at least three variables: (1) the intensity of daylight penetrating the canopy (q,q') in relation to the intensity of the unobstructed sun (Q); (2) the percentage of floor in shade and in sun ((1—S), S); and (3) the areas shaded and sunlit ((A—P), P). For this reason the resultant E. L. U.'s are compound units of a different order than the individual factors involved, and the curves represent the expression of all of the combined factors. The E. L. U., then, becomes a combination which expresses quantitatively the light relations to which organisms on the forest floor are exposed at a given time.

The work of Cowles (1899, 1901), Fuller (1911, 1912, 1912a), Graham (1927) and others has shown the existence of a well defined upland forest-on-sand sere in the area studied, and Shelford (1913) has demonstrated that the animals inhabiting these forest communities are arranged in corresponding seral aggregates; Holmquist (1926) has furthered our knowledge of hibernating invertebrates in this area.

To determine the degree of correlation possible at this time between the several space-illumination factors discussed here as a unit (E. L. U.), and the distribution and activity of the animals resident in these forest communities in the Chicago area, the Coleoptera were used as a test group (Park, 1928, 1929, 1929a, 1929b). Ecological data gathered over six years on the Coleoptera of the Chicago Area (Park, 1930, 1931, 1931a) indicate that (1) there is a bettle sere corresponding to the upland forest-on-sand sere, (2) that definite seasonal succession (aspection) exists throughout the year, (3) that this seasonal periodicity is expressed in an abbreviated and condensed form by the lower beach drift of Lake Michigan, (4) that hibernation is a rhythmic seasonal occurrence in certain species of beetles, in which daylight intensity or possibly the relative length of day and night may play some part, (5) that the colonizing flight or swarming aggregation of a termite, *Reticulitermes tibialis* Banks, in the Chicago area occurred twice on different years towards the end of March, from 11:00 A.M. to 2:00 P.M. when the daylight intensity was more or less at a maximum for the day, normal for the time of year, and accompanied by a fairly constant complex of temperature and relative humidity (Park, 1929b), (6) that the seasonal distribution of the beetles of this sere follows a regular sequence of events which is probably closely correlated with food and with shelter, (7) that many species of beetles are directly dependent upon vegetation for sustenance and therefore indirectly dependent upon light for their distribution, (8) that about one-third of the species of beetles of a forest community live in or on the floor during at least a part of their annual cycle, and are subjected to daylight as has been measured by the writer in terms of foot-candles and the percentage of the area in shade and in sun-flecks, (9) that the fungus community parallels the more extensive forest community in both its seral and seasonal succession, and in passing through intergrading stages of decay which are similar to those stages passed through by logs on the forest floor, and culminating in a mounding condition, and finally (10) that light is an important factor in the ecology of forest Coleoptera indirectly, and probably in part directly in governing their distribution and activity.

The curves in Figure 13, although based on the data for one year, show how the communities of the upland forest-on-sand sere of the Chicago area vary with respect to light:—(1) The cottonwood and conifer communities are both pioneer in character, and fall closer together than to the more mesophytic communities. (2) The conifer associes is remarkably constant, as would be expected from its evergreen nature. (3) The deciduous communities in general resemble each other with respect to the sequence of events throughout the year and the curves for these communities are similar in character. (4) During the period of foliation the four communities studied have E. L. U.'s which are expressed in the succession order of the sere:

cottonwood, conifer, black oak, and climax sugar maple. (5) Each community has a definite range of E. L. U.

The E. L. U. for each community studied was found to vary within certain limits, the lower limit for each community being determined by the portion of the unit area in the unobstructed sun. During the period of foliation (summer) the deciduous communities approach the lower limit of their respective ranges. The theoretical lower limit for any community would be the condition in which there was no light under the trees, and the only light would be, therefore, that falling on P. The value of the E. L. U. in this case is P/A. This becomes clear when the original formula is divided through A, in which case:

$$\text{The E. L. U.} = \frac{P}{A} + \frac{(1-P/A)\ (Sq' + (1-S)q)}{Q}$$

Under the conditions stated, q and S become zero, and the second term of the above equation becomes zero.

The theoretical upper limit would be the condition in which there was all the light available beneath the trees, in which case sq' approaches Q, and (1—S)q approaches zero, and the value of this upper limit is then:

$$\text{E. L. U.} = \frac{PQ + (A-P)Q}{AQ}, \text{ or } \frac{AQ}{AQ} = 1$$

The ranges for the individual forest communities are, then, found to be:

	Ecological Light Units
Pioneer Cottonwood	.840 to 1.000
Pioneer Conifer	.774 to 1.000
Pioneer Black Oak	.354 to 1.000
Climax Sugar Maple	.000 to 1.000

Viewing the upland forest-on-sand sere as a whole, when there is no shade and the whole area is exposed to sunlight, then P=A and A—P=O. Therefore both upper and lower limits are 1. When the entire area is covered by a uniform and unbroken canopy, P=O and the upper limit is 1 and the lower limit is zero.

The Ecological Light Unit as presented is an unweighted one. Only experimental analysis can determine the relative importance of the different space-illumination values which it summarizes. It is possible that this method of formulation can be extended indefinitely for the various ecological factors of an environment, *viz.:* the Ecological Temperature Unit, Ecological Rain Unit, etc. Logically, all the significant factors can be combined into a single formula, the Ecological Environmental Unit. Such a formula might be used to express the action of the environment, or its potentialities upon a collection of individuals or species. Employing this method, the "environ-

mental resistance" (Chapman, 1926, p. 81) of each community in a sere might be attacked from a comparative point of view. Such complex environmental units would need weighting as a result of experimental work designed to test the relative importance of their components before they could be of value.

9. SUMMARY

The data presented in this paper become ecologically significant when interpreted in the light of present knowledge of seral and seasonal succession in the communities studied *i.e.* those of the upland forest sere of the Chicago area. The intensity of daylight, as finally received by the earth, follows a regular sequence of events. The intensity of the unobstructed noonday sun varies with the time of the year and the condition of the atmosphere, but averages over 1000 foot-candles in winter, and following this low period climbs steadily to a peak of about 10,000 foot-candles in late summer, after which the intensity gradually falls.

The communities of deciduous trees show a similar cycle, shaded areas of the pioneer cottonwood having a range of 400 to 4000 foot-candles, those of the pioneer black oak from 200 to 3000 foot-candles and the shade of the climax maple from 40 to 2500 foot-candles. It should be understood that these figures are frequently exceeded on either side of the general range, but these ranges represent the significant averages (see Table III). Also, the daylight intensity cycle for any of these deciduous communities is in general the reverse of the intensity cycle for the open sun, since the period of greatest intensity of the latter (late summer) comes at the time of maximum foliage, and consequently of relative minimum light intensity on the floor of the forest. Shaded regions of the pioneer Conifer community have a more constant range, from approximately 500 to 800 foot-candles. Usually the intensity is lower than that found in the pioneer cottonwood, but higher than that of the pioneer black oak, falling in between these two associes in the growing season (Fig. 10). In winter there is a tendency for the snow to bank upon the pine and juniper needles, lowering the intensity on the floor still further. However, the shaded areas of the conifer associes present the most constant conditions of floor intensity of any of the communities studied.

It should be noted, therefore, that the daylight intensity as admitted to the forest floor, has a characteristic range and course for each well-defined community. In the deciduous forest communities the mean intensity and the percentage of shade vary with the thickness of the forest canopy (the former inversely, the latter directly), following the vernal appearance, autumnal increase in opacity and shedding of leaves. In the evergreen communities the daylight intensity and the percentage of shade are more constant throughout the year.

The factors concerned in intensity of daylight, and the percentage of floor shaded and sunlit, and of density of stand have been combined into a

formula to express their composite action. This figure is quantitative, is termed the Ecological Light Unit (E. L. U.), and its ecological significance has been discussed.

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Statement of ownership, management, circulation, etc., of ECOLOGICAL MONOGRAPHS, published quarterly at Durham, N. C., by the Duke University Press.

Managing Editor: A. S. Pearse.
Business Manager: Ernest Seeman.
Owners: Duke University Press, Durham, N. C.

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